ECOLOGY OF BIRCH LITTER DECOMPOSITION AND FOREST FLOOR PROCESSES IN THE ALASKAN TAIGA

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By

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ECOLOGY OF BIRCH LITTER DECOMPOSITION AND FOREST FLOOR PROCESSES IN THE ALASKAN TAIGA

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Abstract

Our view of an ecological process is influenced by the scale of our hypotheses and experiments. The forest floor can be examined as a *system*, where processes that affect ecosystem carbon and nutrient cycling are controlled by macroscale variables (seasonal climatic changes), which in turn affect microscale controls over microbial activity. In the forest floor of Alaskan taiga, annual layers of *Equisetum* (horsetail) litter demarcate cohorts of birch litter. We collected samples of the forest floor monthly during September 1992, and in June–September 1993. Forest floor material was separated into each of the three most recent litter cohorts, plus the Oe layer, and the Oa layer. Overall, respiration potential decreased with depth of litter (litter age), but showed no change over time. Nitrogen mineralization potential increased with depth, and fluctuated over time. Microbial biomass did not vary with depth, but did increase greatly in September in conjunction with increased litter moisture. Litter C:N ratio decreased with time and varied with depth according to the year-to-year variation in litter quality. Our hypothesis that microbial activity on a particular litter cohort is a function of the litter quality, the vertical position of the litter in the forest floor, and the timing of the observation within seasonal macroclimatic cycles was supported.

The distribution of some taxa of soil fauna correlated with depth. In these cases, the fauna were likely constrained mostly by differences in the microclimate of the forest floor strata. Other soil fauna varied over time, likely in response to differences in the microbial community. Yet other faunal distributions showed an interaction between depth and time, apparently responding to a combination of changes in microclimate and changes in food availability. The creatures that live in water pores may also have responded to an increase in habitat space as the topmost litter strata became wetter. "Cascading" microcosms containing material from these forest floor strata showed a temporary suppression of respiration by leachates from the newer litter on underlying forest floor material. Traditional lit-

terbag techniques were also used to show changes in nitrogen that indicate winter microbial activity.

And so, from hour to hour, we ripe and ripe,

And then, from hour to hour, we rot and rot;

And thereby hangs a tale.

William Shakespeare
As You Like It
Act II, Scene VII

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Except for the Introduction and Conclusions, the chapters of this thesis were written as separate manuscripts intended for publication. When they are submitted for review, J.P. Schimel, M.W. Oswood, and J.M. Anderson will be acknowledged as coauthors.

Introduction

Studies of ecological processes may be of interest because of the importance of the processes examined, their geographical setting, or the scale of the observations. Examination of interactions between these characteristics can be particularly illuminating. The research presented here (of interest from all these factors) examines decomposition and nutrient cycling in the taiga forest floor of Alaska.

In this research, the forest floor is examined as a *system*, in which a variety of processes occur that affect ecosystem carbon and nutrient cycling and nutrient availability for plants. The forest floor is here treated as the 3-dimensional environment in which decomposition takes place, in which nutrients are released from plant detritus for plant uptake or leaching, and in which C is stored and respired to the atmosphere. The forest floor is the site where the macroscale variables that drive processes at a landscape-scale meet the microscale variables that regulate microbial physiology. The forest floor is the system—and the ecological scale—in which the interactions between decomposer microbes, soil fauna, and trees occur.

The research presented here examines forest floor processes in which patterns of macroclimatic influence microclimate, patterns of microclimatic influence microbial biomass, and patterns of microclimate and microbial biomass influence the distributions of soil fauna. I discuss how changes in the quality of decomposing litter may affect the introduction of root-mycorrhizal assemblages and how cohorts of litter at different stages of decomposition can interact, through leachates and *via* fungal hyphae. I will also show how yearly differences in litter quality and winter climate affect microbial processes and the timing of nutrient release. In this thesis I will propose a state-factor model for the control of microbial processes within the birch forest floor.

The taiga

The taiga is a large biome (17% of the earth's land surface and 33% of Alaska), with sizable carbon stores (13% of the planet's soil carbon pool [Post et al. 1982]), and vast quantities of timber. The taiga—a biome with low energy inputs—is likely sensitive to changes in climate. Taiga covers large areas of North America and Eurasia, extending as far south as 45°N in eastern Siberia and as far north as 70°N in Scandinavia and central Siberia. The climate of this region is characterized by short, warm summers and long, cold winters. Soils are generally cold and permafrost is common. Plant communities are strongly influenced by topographic features, such as slope and aspect, because of low soil temperatures and the low sun angle (Kimmins and Wein 1986). In the taiga, large changes in microenvironment occur over shorter distances than in temperate forests (Van Cleve et al. 1983).

Thorough descriptions of the Alaskan taiga are available in Van Cleve et al. (1983) and Van Cleve et al. (1986). In interior Alaska, the taiga contains only six tree species (Table 1), as well as numerous woody and herbaceous shrubs (most notably *Salix*, *Alnus*, *Vaccinium*, and *Rosa*).

Table 1. Tree species of the taiga of interior Alaska

Paper Birch	*Betula papyrifera* Marsh.
Quaking Aspen	*Populus tremuloides* Michx.
Balsam Poplar	*Populus balsamifera* L.
White Spruce	*Picea glauca* [Moench] Voss
Black Spruce	*Picea mariana* [Mill.] B.S.P.
Larch	*Larix laricina* [DuRoi] K. Koch

Because of recurrent patchy fires, the upland taiga is a mosaic of stands of different ages. Fire history and the timing of recruitment interact with slope, aspect,

and drainage, to determine forest types (Van Cleve et al. 1983). Flooding in the lowlands and fire in the uplands reset the successional clock. Insect and mammal herbivory also contribute to forest patchiness.

Paper birch and quaking aspen are typical early to mid-succession tree species in the south aspect of uplands (Figure 1). The understory consists of prickly rose (*Rosa aricularis* Lindl.) and horsetail (*Equisetum arvense*). Clumps of alder (*Alnus crispa*) occur in disturbed areas and in the understory of most mature forests. White spruce seedlings may be present, but because of slow growth, they long remain inconspicuous. Birch and aspen typically dominate a site for 50 to 100 years, but are gradually replaced by white spruce. As stands transit from hardwoods to conifers, feather moss (*Helicomium splendens* [Hedw.] B.S.G.) begins to cover increasing portions of the forest floor (Van Cleve and Yarie 1986). The moss layer insulates the underlying mineral soil, cooling and allowing the formation of permafrost on lowland and north-facing upland sites. Permafrost is absent from south aspects and from the active portion of the river floodplain.

The climate of interior Alaska consists of cold winters and warm summers. The mean temperature in January is –24.5°C, in July +17.5°C, and the mean annual temperature is –3.5°C (Van Cleve et al. 1991). Fairbanks has an average of 151 snow-free and 97 frost-free days (Van Cleve et al. 1991). Cumulative soil degree days (the sum of average daily temperatures above 0°) have been measured as 967–1019 per year at an south-facing upland birch site, compared with 1048–2217 in an upland aspen site and 488–761 in a north-facing upland black spruce (Viereck et al. 1983).

The climate in interior Alaska is semi-arid. Annual precipitation is low (285 mm at Fairbanks, 35% of which falls as snow) but highly variable (Van Cleve et al. 1991). The potential evapotranspiration is 475 mm, which yields an annual precipitation deficit of 190 mm (Van Cleve et al. 1991).

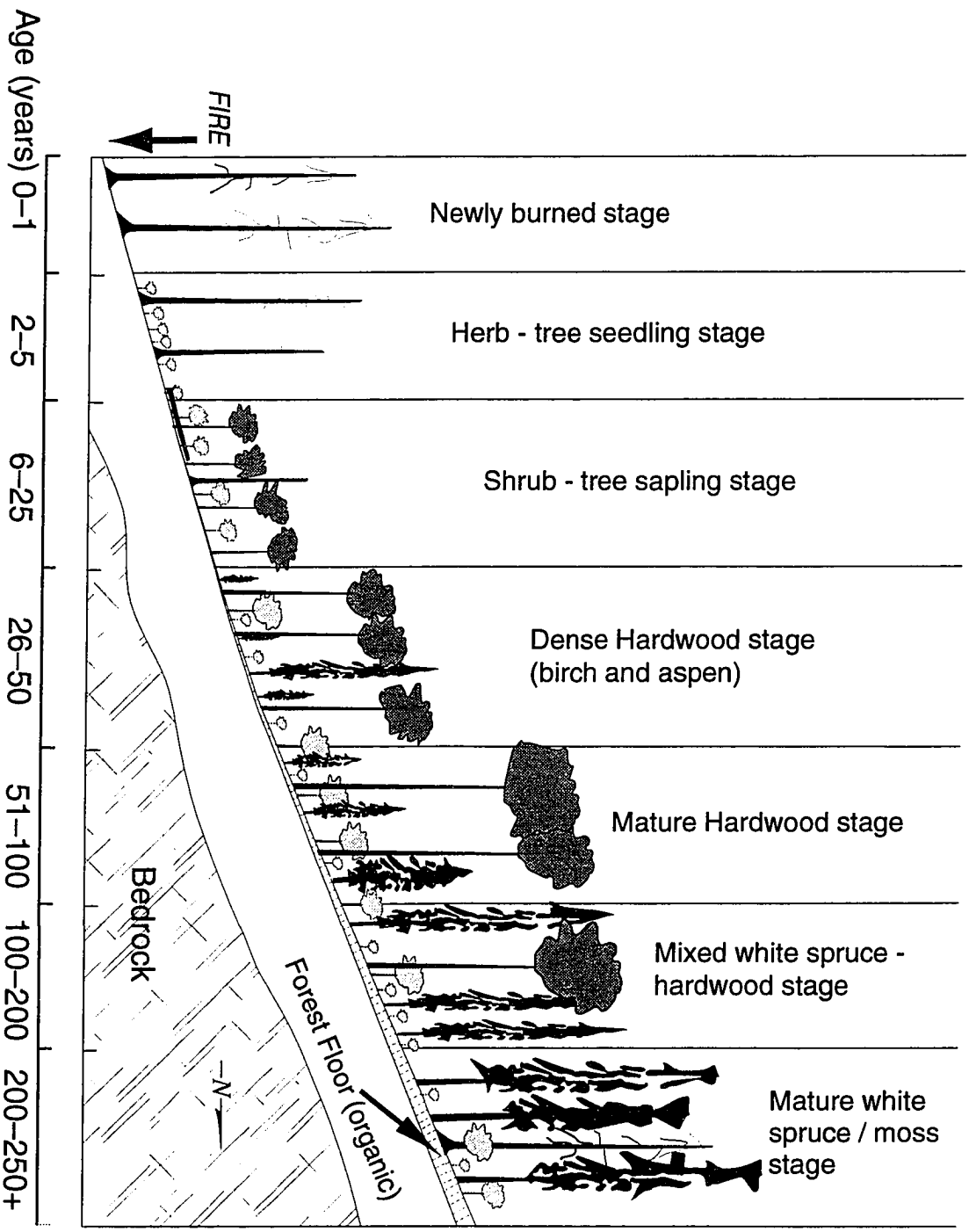

Figure 1. Schematic of south aspect upland succession in the Alaskan taiga. Figure courtesy of G. Juday.

Decomposition processes

As will be stated— repeatedly, our view of an ecological process is strongly influenced by the scale at which we frame our hypotheses and conduct our experiments. According to the model described by Swift et al. (1979), the process of decomposition is regulated by the combined effects of the physical and chemical environment acting with detritus quality on decomposer microbes and faunal communities. These factors control the processes at all scales from cell to biome, although our ability to perceive these factors changes as the scale changes.

The relative importance of climate and resource quality in decomposition, along with the composition of the decomposer community, are broadly functions of geography. In interior Alaska, among-site differences in rate of litter decomposition are controlled more by litter quality than by the site microclimate. The loss of mass from birch litter, for instance, is six times faster than from black spruce litter (Flanagan and Van Cleve 1983, McClaugherty et al. 1985). Differences in decomposition rates among sites with the same species, however, are likely controlled by microclimate.

Litter quality from trees of the same species can vary from year to year. Green birch foliage contains about 2% N by dry weight. Before leaves fall, >50% of the foliar N is recovered by the tree or leached as throughfall. If more N is available for plant uptake from the forest floor, less is translocated from pre-senescent leaves (Flanagan and Van Cleve 1983). Anything that interrupts translocation—an early snowfall, for instance—can greatly affect the N content of the litter that falls to the ground. Indeed, the activity of above-ground herbivores can also affect litter quality. Moderate browsing by moose increases foliar N and the leachability of tannins in birch litter (Irons et al. 1991), thus increasing decomposability. In contrast, insect defoliation causes a decrease in litter N and an increase in phenolic compounds (Bryant et al. 1991), making litter more resistant to decomposition.

Perhaps the most common method for the study of leaf litter decomposition is the use of litterbags (Crossley and Hoglund 1962, Bleak 1970, Lousier and Parkin-

son 1976, Flanagan and Van Cleve 1983, and many others). In this method, litter is placed in mesh bags and left on (or in) the ground for a period of time. The litterbag is later retrieved and the litter analyzed for mass loss, as well as chemical and biological characteristics.

Just such a study is currently being conducted as part of the National Science Foundation Long-term Ecological Research (LTER) program at the Bonanza Creek Experimental Forest near Fairbanks, Alaska. A 10-year litter decomposition study was designed encompassing three successional stages in the upland (post-fire [UP1], birch and aspen [UP2], and white spruce [UP3]). Data from the first three years of this study are available and provide background information about birch litter decomposition which will be useful in later discussions.

These litterbag data presented here are from a mature birch stand in the uplands (UP2A). This discussion will be limited to this one site for the sake of simplicity and because it clearly illustrates the trends of interest. Figure 2, shows a tight correlation ($r^2 = 0.89$) between C loss from birch litter and decompositional time. Data points from June and July are above the regression line, whereas data from August and September are located below the line. This suggests that the activities of decomposer organisms are more intense in late summer when the weather usually is rainy than in early summer when it is dry. Although the relationship is quite strong, should we expect chronological time to be the best predictor of C loss from litter? We can speculate that from the perspective of a decomposer organism, time measured by the ticks of a clock would be an abstraction. If we replace chronological time in our analysis with cumulative soil degree-days (Figure 3), we see an even tighter relationship ($r^2 = 0.96$). Cumulative soil degree-days is an index of decompositional time that only considers summer climate, disregarding winter, when decompositional processes slow. Yet, early summer is generally warmer than late summer when C loss is most rapid. The moister conditions of late summer probably account for much of the remaining variance in the regression.

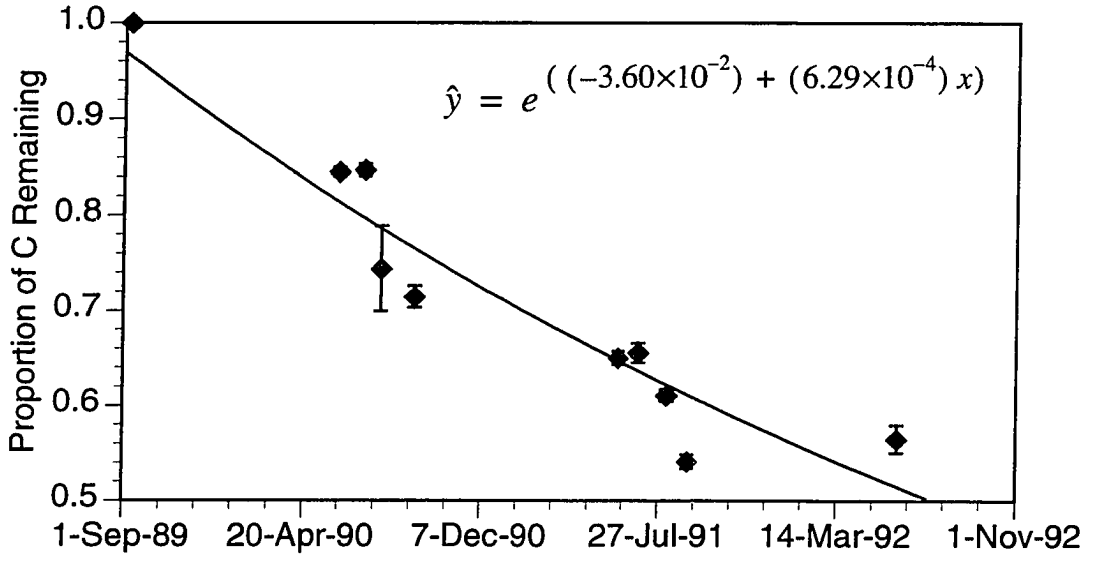

Figure 2. Mean carbon loss from birch litter over time at an upland birch stand (UP2A) in the Bonanza Creek Experimental Forest, Alaska. Fitted curve is an exponential function ($r^2 = 0.89$), Symbols obscure some standard error bars.

As C was lost from litter over decompositional time, the absolute quantity of N in the litter increased (Figures 4 and 5). Eventually the C:N ratio narrowed enough so the decomposer community became C, rather than N, limited and began to mineralize N. Litter C:N ratio narrowed, as the litter lost C and acquired N (Figure 6).

The litterbag technique is quite valuable because it allows us to estimate process rates, such as mass loss and nutrient mineralization. This technique can also allow the researcher, through a reciprocal transfer design, to separate litter-quality effects from site-related effects of climatic in the control rates of decomposition and nutrient cycling (Flanagan and Van Cleve 1983, McClaugherty et al. 1985). Because the litter bag approach follows the fate of one litter cohort as it passes through the forest floor over time, it does not, therefore, allow us to simultaneously examine the status of all the cohorts at different decompositional stages, and determine how they might interact. The line of decompositional time drawn for us by a litterbag study may indeed be spatially or temporally orthogonal to forest floor processes of interest, such as changes in microbial biomass or internal nutrient cycling.

Birch litter decomposition does not occur in isolation. This process happens on and in the forest floor. The forest floor is not a simple sink for released elements. As we have seen from the previous data, N moves both into and out of litter as it decomposes. This movement implies N cycling within the forest floor but does not describe the source for N. Further, decomposition processes can be sensitive to the dynamics of microbial and faunal populations. Litterbags are a poor method for evaluating these dynamics. To develop the complete picture of decomposition processes requires simultaneously examining changes in litter and decomposer organisms at varying decompositional stages and vertical locations within the forest floor over time. This research, therefore, considers the forest floor as a physical, chemical, and biological environment, and examines the processes

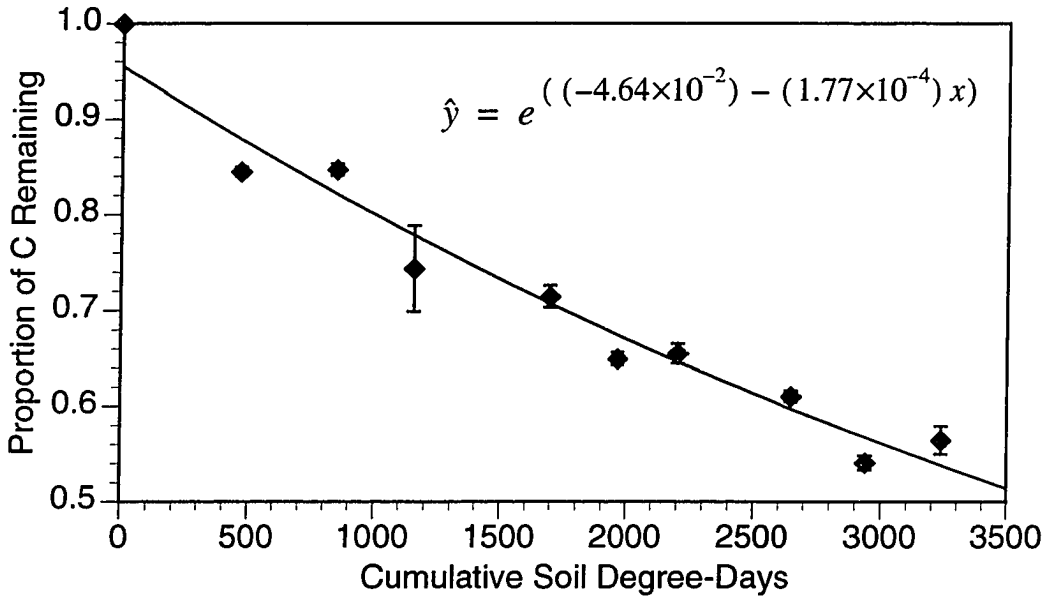

Figure 3. Mean carbon loss from birch litter as soil degree-days accumulate over the interval of study at an upland birch stand (UP2A) in the Bonanza Creek Experimental Forest, Alaska. Fitted curve is an exponential function ($r^2 = 0.96$). Symbols obscure some standard error bars.

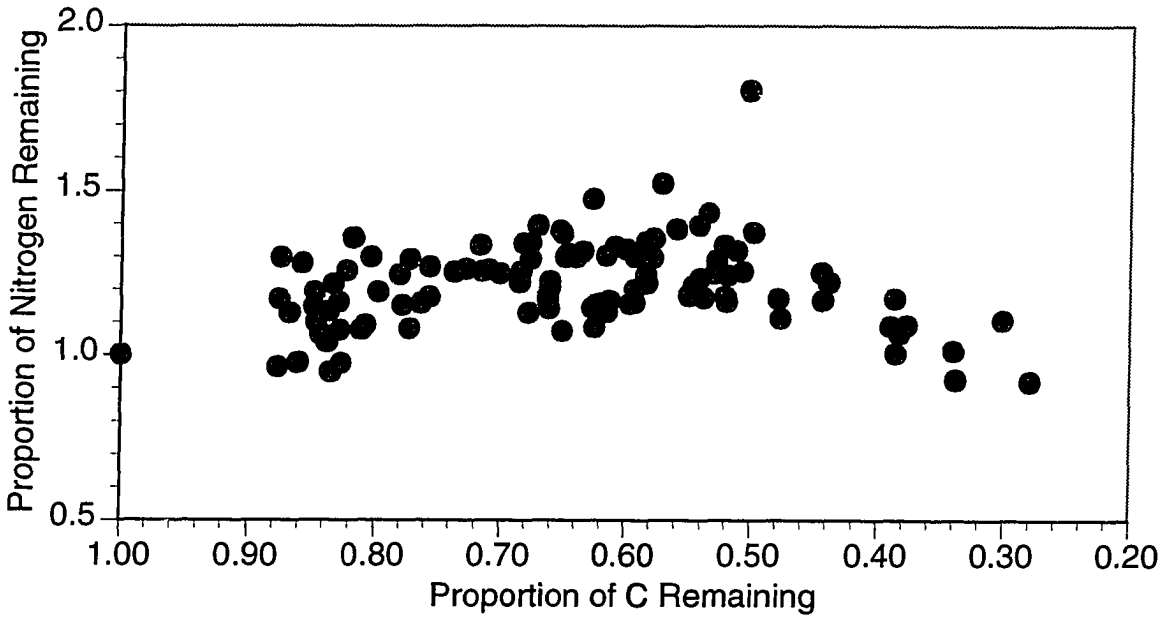

Figure 4. Changes in the N content of birch litter as it loses C at an upland birch stand (UP2A) in the Bonanza Creek Experimental Forest, Alaska.

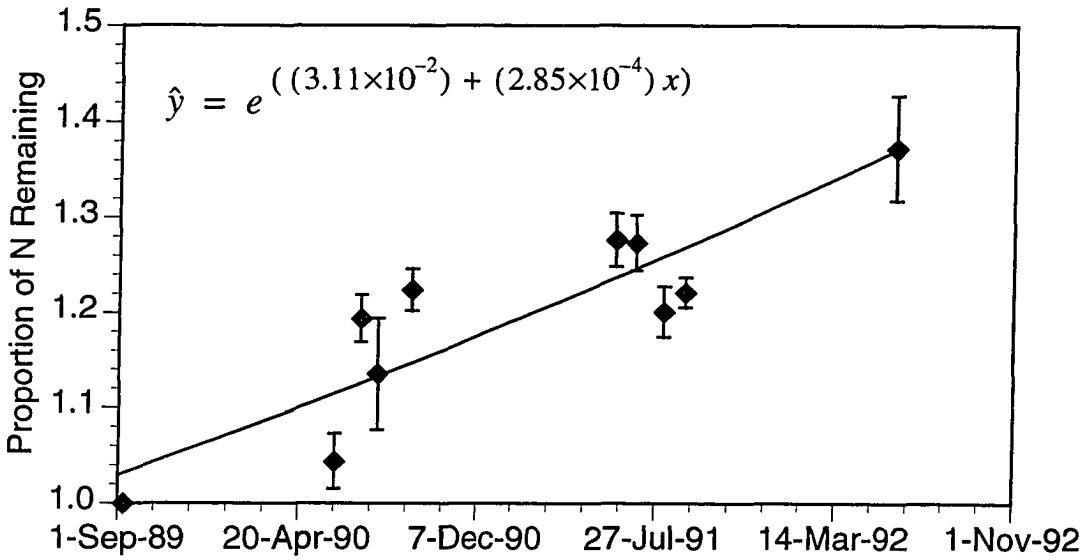

Figure 5. Mean nitrogen gain of birch litter over time at an upland birch stand (UP2A) in the Bonanza Creek Experimental Forest, Alaska. Fitted curve is an exponential function ($r^2 = 0.74$).

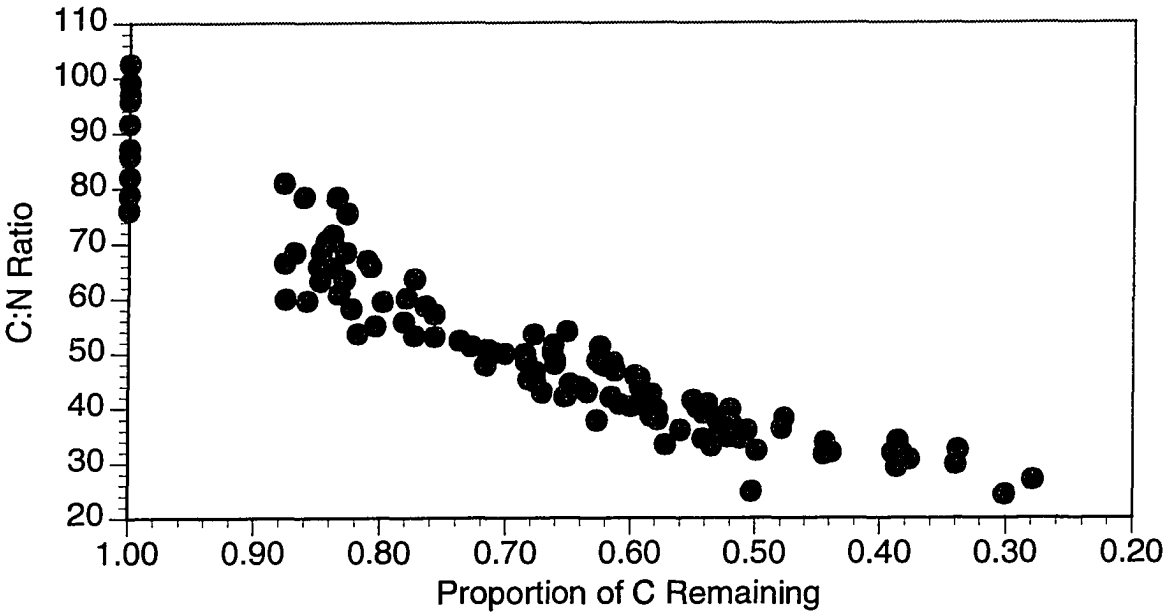

Figure 6. Changes in C:N ratio of birch litter as it loses C at an upland birch stand (UP2A) in the Bonanza Creek Experimental Forest, Alaska.

of decomposition and nutrient release within the context of the cycles and gradients within that environment.

This research examines the following model for forest floor function: vertical, incremental changes associated with discrete litter cohorts, overlain by continuous changes within the cohorts over time and cyclical changes in soil climate define the patterns of C and N release from that litter and the patterns N availability for plant uptake.

The research presented in this thesis used a new approach for simultaneously examining the chemical, microbial and faunal characteristics of most recent cohorts of decomposing litter, as well as other forest floor horizons. "Cascading" microcosms containing material from these forest floor strata were then employed to examine the effects of leachates from the newer litter on microbial processes of underlying forest floor material. Traditional litterbag techniques also were used to examine the interaction of litter quality and climate on microbial processes under the snow.

Site description

The study was conducted at the Arboretum of the University of Alaska Fairbanks, adjacent to the university campus in Fairbanks, Alaska (64° 51' 36" N, 147° 50' 24" W). The site consists of a near-uniform 100–130-year-old stand of paper birch (*Betula papyrifera*) on the top of a ridge at 144 m elevation. Stands of this age typically have a density averaging 575 trees · ha^{-1} and an average basal area of 25 $m^2 \cdot ha^{-1}$. Tree biomass, annual production, and litterfall average 11156, 470, and 251 $g \cdot m^2$ respectively (Viereck et al. 1983). A thick growth of *Equisetum arvense* (horsetail) covers the forest floor. The soil at this site is an alfic cryochrept.

In the forest floor, *Equisetum* litter forms a marker—a natural litterbag—separating the three most recent year-classes of birch litter (the age 0+, 1+, and 2+ litter. These three cohorts taken together made up the Oi layer. Below the age 2+ litter, *Equisetum* litter, as a marker of annual layers, broke down. The Oe horizon

consisted of the distinct layer of material made up of leaf parts. Below this was a sharp transition into a zone of fibrous material with few, if any, recognizable leaf parts. The entire organic layer—Oi, Oe, and Oa—was 8 to 10 cm thick. Beneath the organic forest floor is a thick layer of loess, which is about 98% inorganic.)

Table 2. Mean mass and proportion of C and N in the birch forest floor, University of Alaska Fairbanks Arboretum, 1993.

Soil Strata	Mass $g \cdot m^{-2}$	Proportion of C	Proportion of N
Stratum 1 Age 0+ litter	243.1	0.463	0.016
Stratum 2 Age 1+ litter	245.3	0.425	0.014
Stratum 3 Age 2+ litter	233.1	0.406	0.015
Stratum 4 Oe layer	468.7	0.362	0.016
Stratum 5 Oa layer	~ 4500	0.282	0.013

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Stratification of soil ecological processes: a study of the birch forest floor in the Alaskan taiga

Our view of an ecological process is strongly influenced by the scale in which we frame questions and the methods with which we study them. At all scales from cell to biome, the physical-chemical environment, resource quality, and the decomposer organisms interact to control the rates of decomposition and element release from plant detritus (Swift et al. 1979). As scales of study increase, it becomes more difficult to associate the activities of specific organisms to specific large-scale processes (Schimel 1995). Perhaps for this reason, decomposition studies often are conducted either at microscale, where cell physiology and food webs are prominent, or at macroscale (ecosystem or landscape), where climate or resource quality, or both, are the overriding controls on rates of element release and decomposer organisms are usually invisible.

The climatic and chemical controls on decomposition are important to the understanding of geochemical cycles on plant productivity. The identification of spatial and temporal patterns of carbon and nutrient mineralization with plant succession (Blair 1988, Flanagan and Van Cleve 1983), across landscapes (Gosz et al. 1973, Berg et al. 1993), or among ecosystems (Insam et al. 1989, Berg et al. 1989) is a common goal of ecosystem-scale studies. Decomposition, from this point of view, has focused primarily on transformations of litter and the elements released.

From the perspective of the organisms that actually do the work, litter is a resource. Decomposition is merely a by-product of their livelihood, and excess inorganic nutrients are wastes. Bacteria and fungi grow on organic compounds and incorporate them into their biomass. Soil fauna mediate microbial breakdown by consuming and thereby increasing surface area of litter, by changing the phys-

ical characteristics of the soil, and by eating the decomposer microbes and each other (Seastedt 1984). At this scale, decomposition dynamics are regulated by the community dynamics of organisms within complex food webs (Elliott et al. 1984, Ingham et al. 1985, Setälä et al. 1991).

Spanning these perspectives is a view of litter decomposition and the associated decomposer trophic webs as components of a general soil milieu. In this perspective, soil—or more specific to this study, the taiga forest floor—is a complex and dynamic system. Carbon and nutrients enter as leaf litter and woody debris from above and root litter and root exudates from below ground (McClaugherty et al. 1982). The detritus composing the forest floor serves simultaneously as an ever-changing substrate and as habitat. There is a succession of microbial (Visser and Parkinson 1975, Klironomos et al. 1992) and faunal (Hågvar and Kjøndal 1981, Siepel 1990) communities as litter is decomposed. Microbes, fauna, and roots interact to control below-ground nutrient cycles (Anderson et al. 1985, Anderson and Leonard 1988, Cheng and Coleman 1990).

From this point of view, climate and litter chemistry interact to affect complex soil community dynamics, which in turn mediate carbon mineralization and nutrient release. Studies at this scale link the activities of decomposer organisms to the processes they enable and to the plants that both provide the litter that drives the system and rely on the end products of its decomposition. At this scale we may determine when, where, and under what controls nutrients are released from decomposing litter and how the nutrients cycle within the forest floor.

Complicating efforts to take this approach is the problem of simultaneously measuring the state factors controlling processes. We may be able to measure a biotic process on a piece of detritus, but it is quite difficult at the same time to relate that process to the chemistry of the litter, to the microclimatic conditions at that particular point in the soil, and to the status of the organisms responsible for the process. To accomplish this, we must view the forest floor in a resolution higher than the classic litter (Oi), fermentation (Oe), and humus (Oa) horizons

used by Van Cleve and Sprague (1971), Federer (1983), Flanagan and Van Cleve (1983), Salonius (1983), and many others. The Oi horizon typically contains litter from more than one yearly leaf crop, and a study of the Oi as a whole necessarily lumps litter of various qualities and decompositional ages. From litterbag studies, we have seen that important transformations occur during the first few years of decomposition. Distinguishing yearly leaf crops (cohorts) and examining them and other strata in the forest floor simultaneously across time is both useful and scientifically exciting.

In interior Alaska, where this study was conducted, climate exerts dominant control over biological activity. Not only is the ground covered with snow and surface organic material $\leq 0°$ C for an average of 214 days per year, but a strong pattern in summer precipitation occurs. Late summer is generally much rainier than early summer. Fungal biomass responds to soil moisture (Moore 1985, Berg 1991), and soil moisture is largely determined by precipitation. How moisture might vary with depth in the forest floor, or how variation in moisture might determine the distribution of microbial biomass is poorly known.

This study: 1) presents a method for discriminating yearly cohorts of litter in the birch forest floor of interior Alaska; 2) examines, over the brief Alaskan summer, a broad range of biological processes occurring in five forest floor layers of different decompositional age; and 3) tests the following hypothesis: Microbial activity on a given litter cohort is a controlled primarily by litter quality, but is modified by the vertical position in the forest floor and seasonal climatic variation. Understanding this process is essential if we are to understand the dynamics of nutrient cycling and C release in the forest floor.

Methods and Materials

This study was conducted at the Arboretum of the University of Alaska Fairbanks, adjacent to the university campus in Fairbanks, Alaska (64° 51' 36" N, 147° 50' 24" W). The site consists of a near-uniform 100–130-year-old stand of paper birch (*Betula papyrifera*) on the top of a ridge at 144 m elevation. Stands of this age typically have a density averaging 575 trees · ha^{-1} and an average basal area of 25 $m^2 \cdot ha^{-1}$. Tree biomass, annual production, and litterfall average 11156, 470, and 251 $g \cdot m^2$ respectively (Viereck, et al. 1983). A thick growth of *Equisetum arvense* (horsetail) covers the forest floor. The soil at this site is an alfic cryochrept.

At the arboretum study site, distinct layers of *Equisetum* litter separate the three newest year classes of birch litter in the forest floor. *Equisetum*, because of its texture and the presence of silica in its tissues, leaves a long-lasting residue that provides a sharp visual contrast with birch litter. The forest floor at this site is a mor soil. Because of the near absence of macroinvertebrates, litter does not rapidly mix with underlying forest floor material and each birch leaf generally maintains its location relative to surrounding litter for 3 to 4 years.

We sampled the forest floor of the arboretum on 9 September 1992, and 1 June, 5 July, 5 August, and 5 September 1993. Supplemental samples were taken on 12 September 1993 for a related experiment. At each date, five replicate samples were taken from random locations within a 10 m square grid. Each replicate consisted of five 0.02 m^2 cores that were taken within 3 cm of each other and composited. To take each core, we placed the corer on the forest floor at the random grid point and cut the forest floor around the corer with a serrated-edge knife. We brought the forest floor material into the laboratory and separated it by strata (Table 2.)

Equisetum litter served as the marker separating the three most recent year-classes of birch litter (the age 0+, 1+, and 2+ litter). Below the age 2+ litter, the annual layers broke down. The Oe horizon consisted of the distinct layer of material made up of leaf parts. Below this was a sharp transition into a zone of fibrous material with few, if any, recognizable leaf parts. The upper 5 cm of this layer was

Table 3. Year classes (the year the litter fell) of the litter comprising the forest floor strata, University of Alaska Fairbanks Arboretum.

	September 1992 samples	June–September 1993 samples
Stratum 1 Age 0+ litter	1991	1992
Stratum 2 Age 1+ litter	1990	1991
Stratum 3 Age 2+ litter	1989	1990
Stratum 4 Oe layer	before 1989	before 1990
Stratum 5 Oa layer	roots and humus	roots and humus

defined as a subsample of the Oa horizon. Material below this was discarded, along with woody debris and coarse roots from all strata. The entire organic layer—Oi, Oe, and Oa— is 8 to 10 cm thick. Beneath the organic forest floor is a thick loess layer, that is about 98% inorganic.

We measured the total fresh weight of the material composing each of the strata and determined gravimetrically the moisture content of a subsample of each stratum. From these, we calculated (for each stratum) moisture as g H_2O per g dry weight and as percent free drainage (water holding) capacity. We calculated free drainage capacity by saturating samples. Material was subsampled using weights at field moisture, but the results of analyses were calculated as dry-weight equivalents.

Respiration potential of subsamples of each litter stratum was measured in the laboratory. The subsamples (1 g each) were placed in 50 ml centrifuge tubes, adjusted to 50% free drainage capacity and incubated at 15°C. Respiration was allowed to stabilize for four days, then the tubes were flushed with air, capped,

and the rate of CO_2 production measured over 3 hours; this rate is the respiration potential. These and all other measurements of CO_2 were done on a Shimadzu GC14a gas chromatograph with a thermal conductivity detector.

On 2 g subsamples from each litter sample, we measured microbial biomass using the chloroform fumigation-extraction technique (Brookes et al. 1985, Tate et al. 1988). In this method, organic carbon and nitrogen is extracted with 0.5 M potassium sulfate from chloroform-fumigated (lysing microbes and releasing microbial C and N) and nonfumigated (control) soil. The extracted organic carbon and nitrogen were frozen and later analyzed, after dichromate digestion, by colorimetry on a Lachat flow injection analyzer. C was measured by the consumption of Cr^{VI} using a semicarbazide dye. NH_4^+ was measured using standard salicylate chemistry (Doyle and Schimel, unpubl. method). N flush data were divided by 0.8 to adjust for the difference in efficiency between the dichromate digestion we used and the standard Kjieldahl digestion (Doyle and Schimel, unpubl. method). C and N flush values were divided by Kc (0.37, Sugai and Schimel 1993) and Kn (0.54, Brookes et al. 1985) corrections for extraction efficiency to obtain estimates of microbial biomass C and N.

On two other sets of 2 g subsamples from each litter strata, we measured nitrogen mineralization potential over a 30-day incubation at 15°C and 50% free drainage (water holding) capacity. Initial and final N concentrations were measured by extracting NH_4^+ and NO_3^- with 2 M KCl and analyzing the extracts colorimetrically using a Lachat autoanalyzer.

A 5 g subsample of each litter was dried at 40°C in a forced-air oven, ground, and stored dry for chemical analysis. The ground litter samples were analyzed for total C and N with a LECO 2000 carbon, nitrogen, and sulfur analyzer.

The supplemental samples taken on 12 September 1993 were dissected into strata as described previously. Subsamples were sealed in zip-lock plastic bags and sent by courier to the Soil Microbial Biomass Service, Department of Botany and Plant Pathology, Oregon State University. The samples were analyzed for

active bacterial and fungal biomass, as well as total fungal biomass using the fluorescein diacetate staining methods of Ingham and Klein (1984). Total bacterial biomass was determined using the fluorescein isothiocyanate staining method of Babiuk and Paul (1970).

Twenty packs, each composed of five undecomposed birch leaves, tied together at the petiole and tethered with monofilament line, were placed under the Age 0+ litter and under the Age 2+ litter on 18 June 1993. The litter packs were paired, so that the packs placed under the Age 2+ litter were directly under and 2 layers down from those placed under the Age 0+ litter. The litter packs were retrieved on 16 September 1993. The residue litter was dried at 40°C, ground, and later analyzed on the LECO 2000 carbon, nitrogen, and sulfur analyzer.

Analyses consisted of nonlinear regression, and one- and two-way analyses of variance (ANOVA). In the one-way ANOVAs, post-hoc tests were conducted using the Scheffé test statistic, and in the two-way ANOVAs, cell-to-cell comparisons were conducted as contrasts within the general linear model. Data used in the ANOVAs were first rank-transformed (Conover and Iman 1981), to compensate for non-normality. Data were analyzed using Systat software (version 5.2).

Results

We express the time scale of decomposition in two ways. Within-year time is shown as the month-to-month changes in chemical and microbial status of the forest floor material. Between-year time is seen in the differences between the year cohorts of litter comprising the forest floor strata. In the bar graphs from September 1992 (Figure 7), between-year time (depth) is displayed on the vertical axis. In the graphic matrices for 1993 data (such as Figure 9), within-year time is displayed along the x axis, whereas between-year time is displayed across the y axes. In presenting the results of analyses of variance, within-year time will be referred to as the "time" effect and between-year time—comparisons between strata—will be referred to as the "depth" effect. These data presented in these graphic matrices are based on one sampling date per month and reflect changes across the summer. These data (apart from the ratios) are expressed as concentrations and do not reflect bulk flows.

Thirty-year average temperatures for the months May–August were evaluated for 1961–1990 (National Weather Service data). The mean monthly precipitation increased from May (1.55 cm) through August (4.98 cm) and then decreased in September (2.41 cm). In 1992, May (3.12 cm), June (5.46 cm), and July (5.89 cm) were rainier than average, whereas August was much drier (1.50 cm). In 1993, July was dry (0.89 cm), August (4.01 cm) was slightly below average, and September precipitation (6.68 cm) was over twice the 30-year mean.

Because forest floor samples were always taken once during the first week of the month, the litter moisture values largely reflect the rainfall of the last days of the previous month. In September 1992, the litter moisture content (g H_2O • g^{-1} dry weight litter, Figure 7a) showed a significant ($p \leq 0.01$) depth effect. Litter moisture was highest in the Age 2+ litter and lowest in the Age 0+ litter. In 1993, litter moisture generally increased ($p \leq 0.01$) from June through September and varied ($p = 0.049$) with depth (Figure 9). The interaction between depth and time was also significant ($p \leq 0.01$). Litter moisture in the top two cohorts was low on

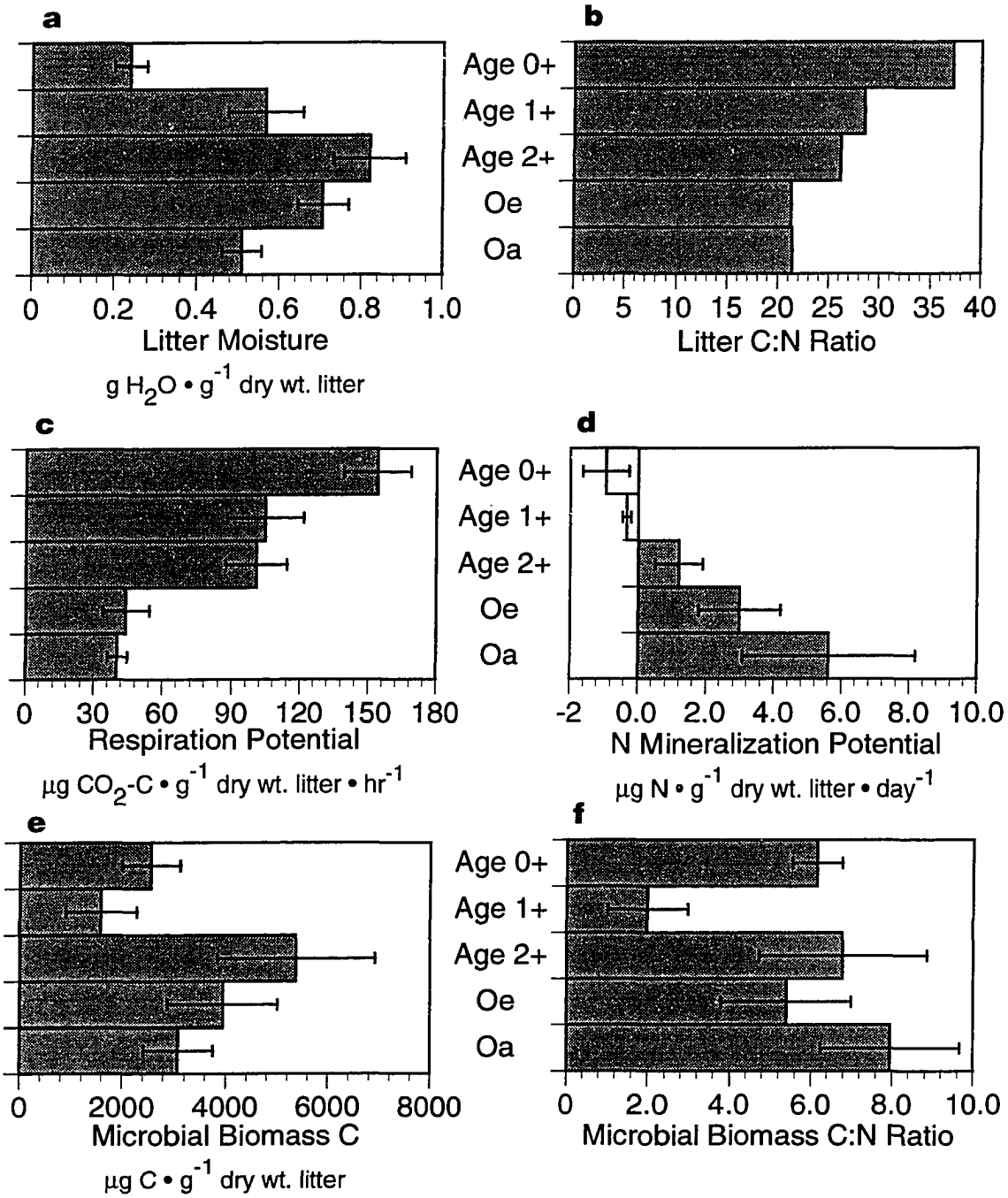

Figure 7. Litter C:N ratio, respiration potential, N mineralization, litter moisture, microbial biomass C, and microbial biomass C:N ratio of forest floor strata, September 1992. Bars represent means and lines represent standard error. Standard errors of litter C:N data are too small to appear on this graph.

the June and July sampling dates. Moisture in these strata increased in August and increased again sharply in September. In the age 2+ litter and the Oe and Oa layers the moisture remained low at the August sampling, before increasing in September. The increase of moisture over time was the greatest in the upper-most strata and lowest in the Oa layer, reflecting water movement down the profile. The different pattern of soil moisture with depth in September 1992 (Figure 7*a*) and September 1993 (Figure 8) is almost certainly because of more rain in August and September 1993 than in 1992.

Litter quality, expressed by the C:N ratio, decreased as birch litter decomposed, because N was immobilized and labile C was respired to CO_2, leaving more recalcitrant compounds. In September 1992, the C:N ratio of the forest floor material decreased significantly ($p \leq 0.01$) with depth (Figure 7*b*). In 1993, the litter C:N ratio (Figure 9) decreased over time ($p \leq 0.01$) and with depth ($p \leq 0.01$). The interaction between time and depth was also significant ($p \leq 0.01$). The Age 0+ litter decreased from a C:N ratio of 35.6 in early June to 20.0 in early September. The largest monthly changes were from August to September in both the Age 0+ and Age 1+ litter. The decrease in C:N over the summer months was largest in the newest litter and the trend became less pronounced with depth. In the Oe and Oa layers the C:N changed little over the course of the summer.

Respiration potential index, decreased as birch litter decomposed. In September 1992, the respiration potential of the forest floor material decreased significantly ($p \leq 0.01$) with depth (Figure 7*c*). In 1993, overall respiration potential (Figure 10) decreased with depth ($p \leq 0.001$) and over time ($p \leq 0.01$). This suggests that the respiration potential index—short-term respiration in the lab under optimal conditions—is a good index of the labile carbon content of the forest floor material (Harris and Riha 1991). No significant interaction occurred between depth and time. In the Age 0+ litter, respiration steadily declined from June through September. The Age 1+ litter began the summer with respiration potential values about one half those of the Age 0+ litter and the values declined

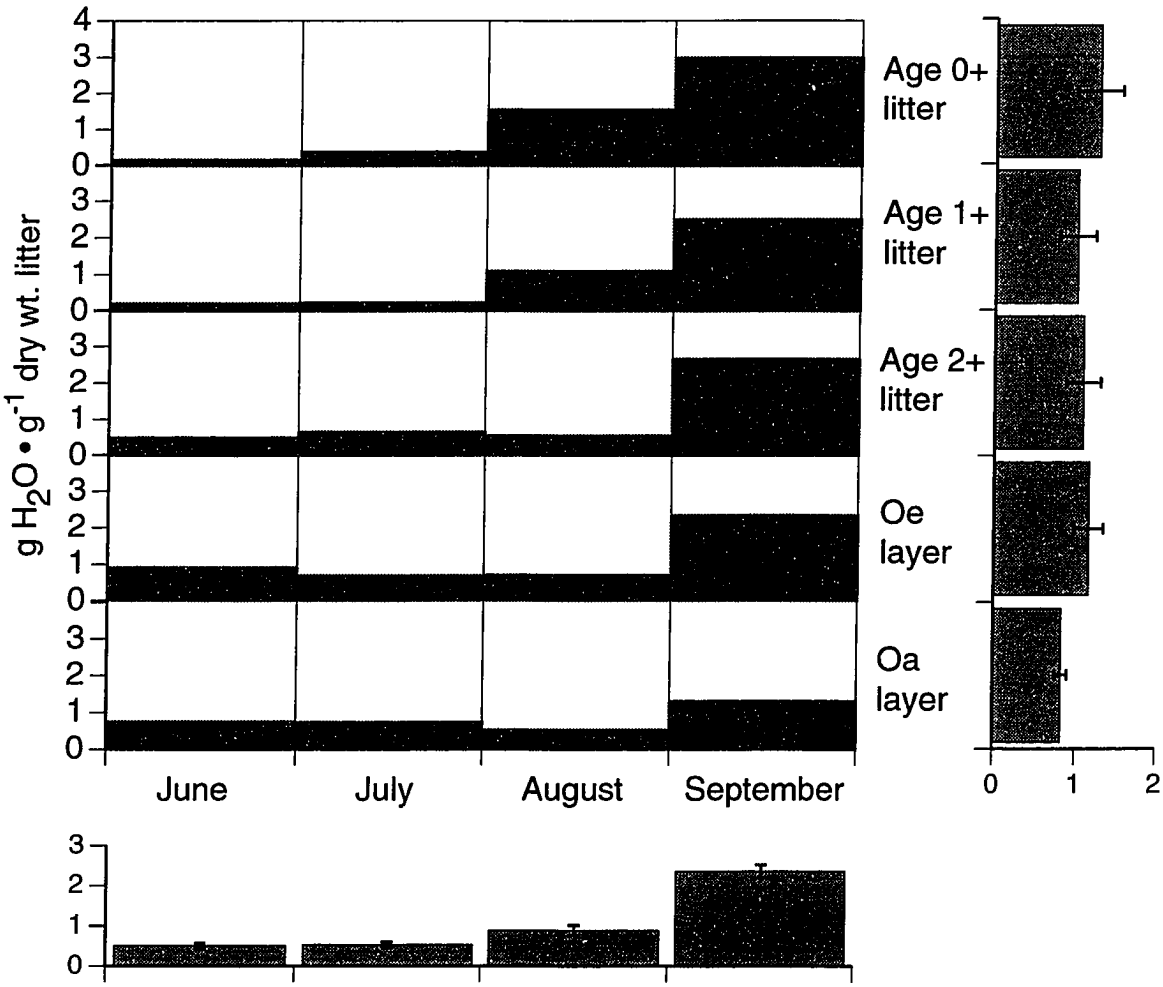

Figure 8. Litter moisture content of forest floor strata, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

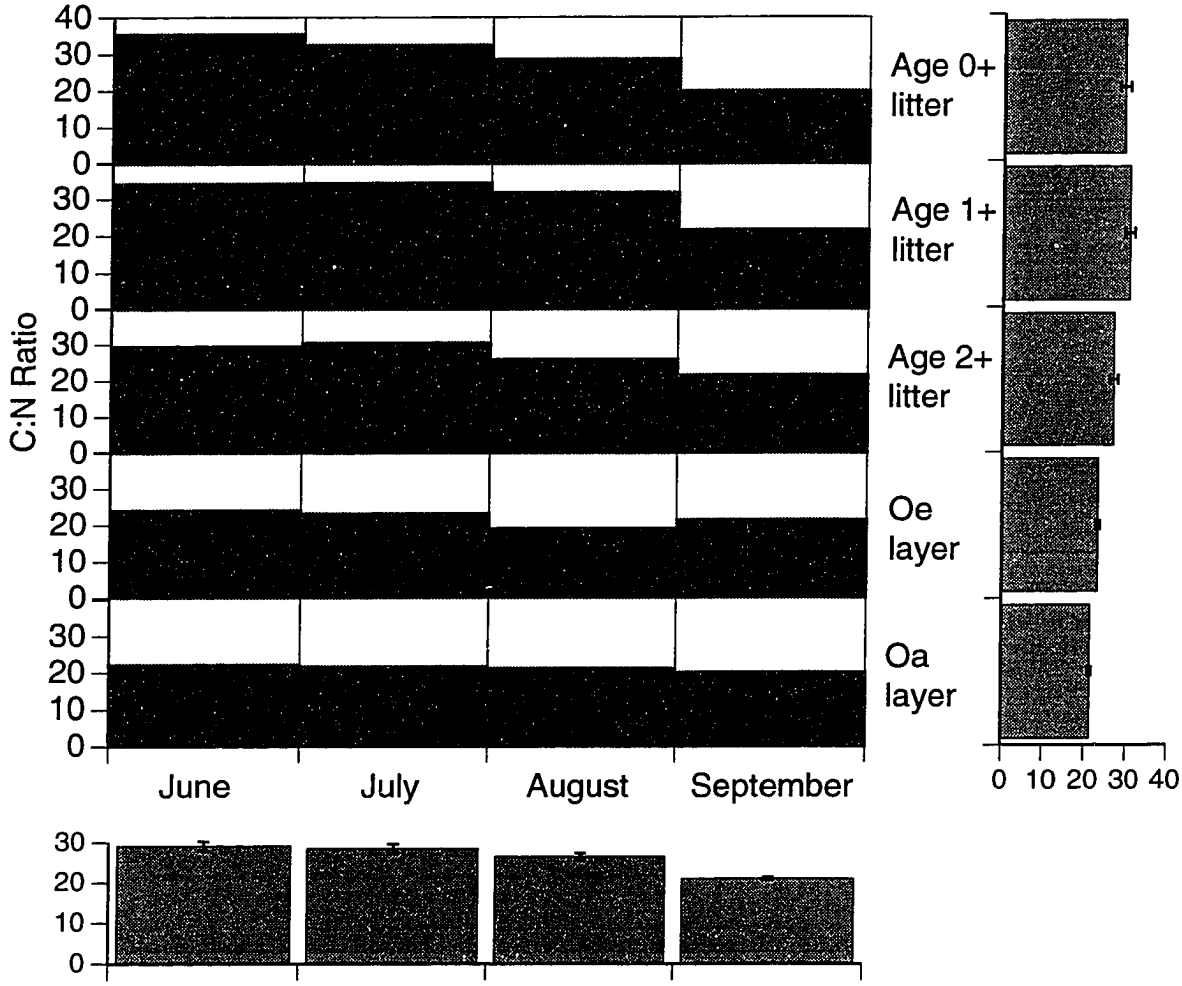

Figure 9. Litter C:N ratio of the forest floor strata, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

through the summer. The Age 2+ litter showed no consistent trend. The Oe layer respiration potential was low, but showed a slight decrease through summer; the Oa layer remained low throughout.

N mineralization potential generally increased as decomposition progressed. In September 1992, N mineralization potential (μg N • g^{-1} dry weight litter • day^{-1}) of the forest floor material increased significantly ($p \leq 0.01$) with depth (Figure 7*d*). In 1993, N mineralization (Figure 11) potential generally increased ($p \leq 0.01$) with depth and showed significant fluctuation but no clear trend over time ($p \leq 0.01$). The interaction between time and depth was not significant. N immobilization was greatest in the Age 0+ and 1+ litter in September. N mineralization potential was positive over all sampling dates in the Oe and Oa layers. There was a pulse in the N mineralization potential in August over all layers.

The pattern of chloroform-labile carbon from microbial biomass (μg C • g^{-1} dry weight litter) was very similar to the pattern of litter moisture. Although in September 1992 (Figure 7*e*), microbial biomass carbon showed no significant depth effect, the highest mean value occurred in the Age 2+ litter and the lowest in the Age 0+ litter. In 1993, microbial biomass C (Figure 12) generally increased over time ($p \leq 0.01$) and decreased with depth ($p \leq 0.01$). There was no interaction between time and depth. Microbial biomass C in all strata was low from June through August and increased in September. The increase in biomass carbon over time was the greatest in the upper-most strata and lowest in the Oa layer.

In September 1992, like microbial biomass C, the microbial biomass C:N ratio showed no significant depth effect (Figure 7*f*). In 1993, as for the litter C:N ratio, the C:N ratio of the microbial biomass (Figure 13) generally decreased with depth ($p \leq 0.01$) and generally decreased with time ($p \leq 0.01$). The interaction between depth and time also was significant ($p = 0.03$). Biomass C:N decreased from June through August in the two uppermost layers, but increased again in September.

Direct counts of microbes were done on the supplemental samples gathered on 12 September 1993. FDA-active fungal biomass (Figure 14*a*) also showed a sig-

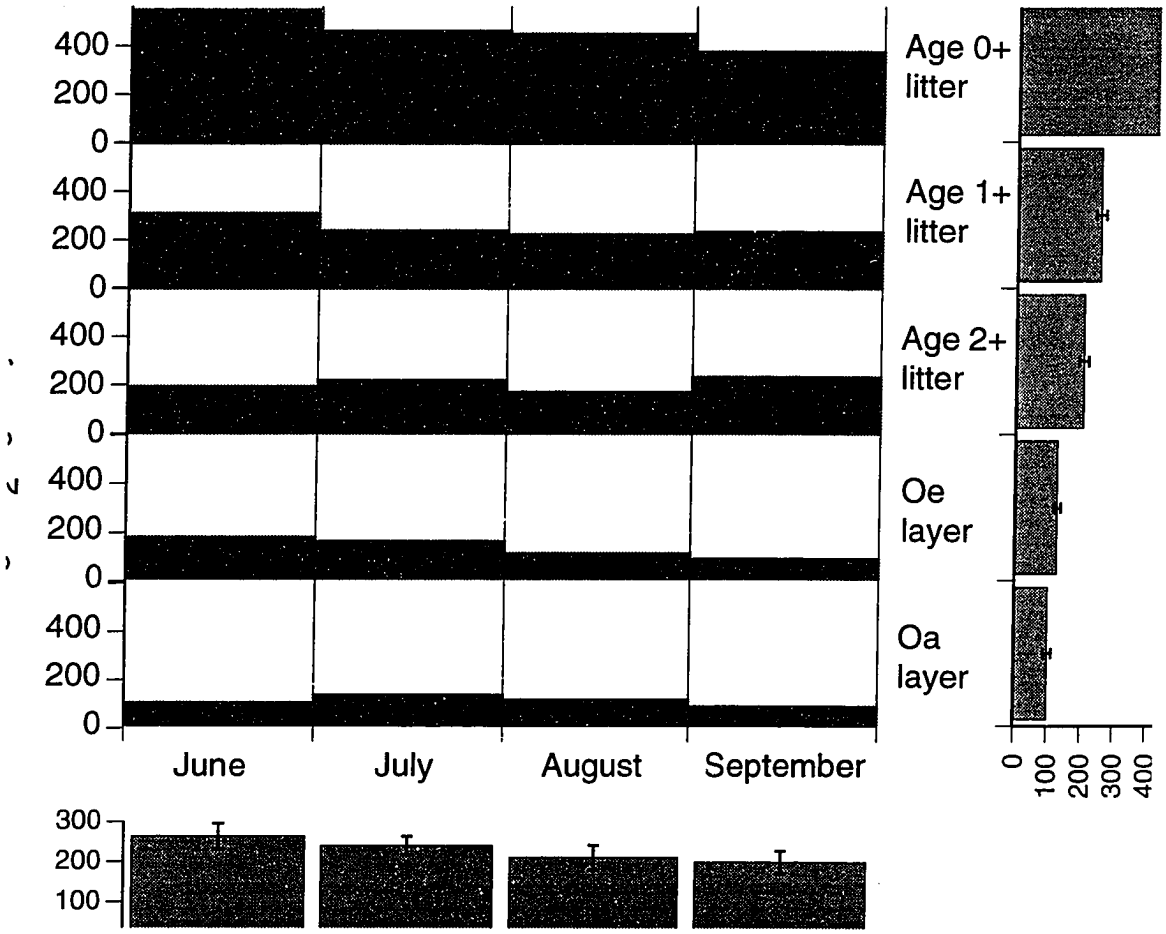

Figure 10. Respiration potential of forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

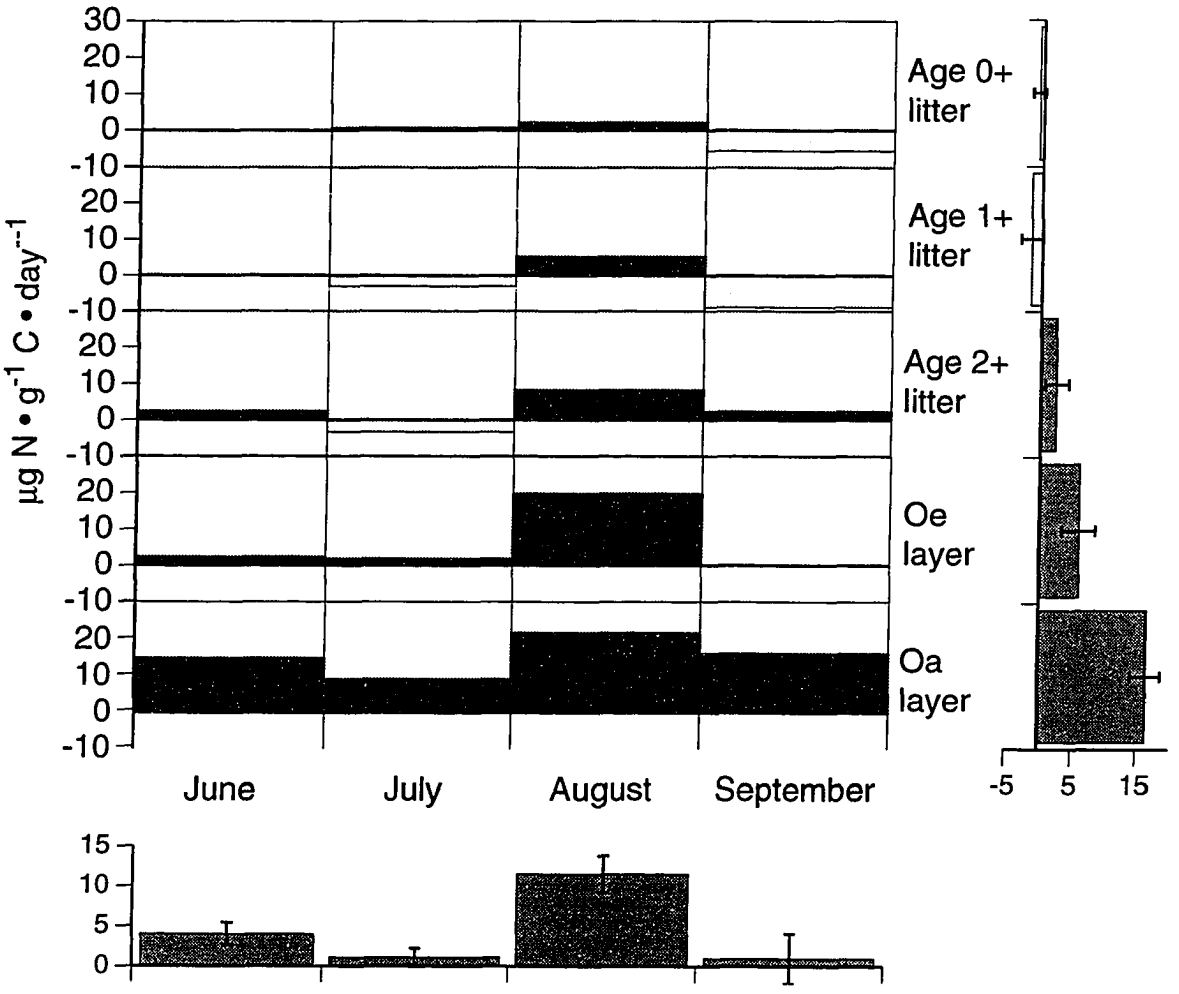

Figure 11. Nitrogen mineralization potential of forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

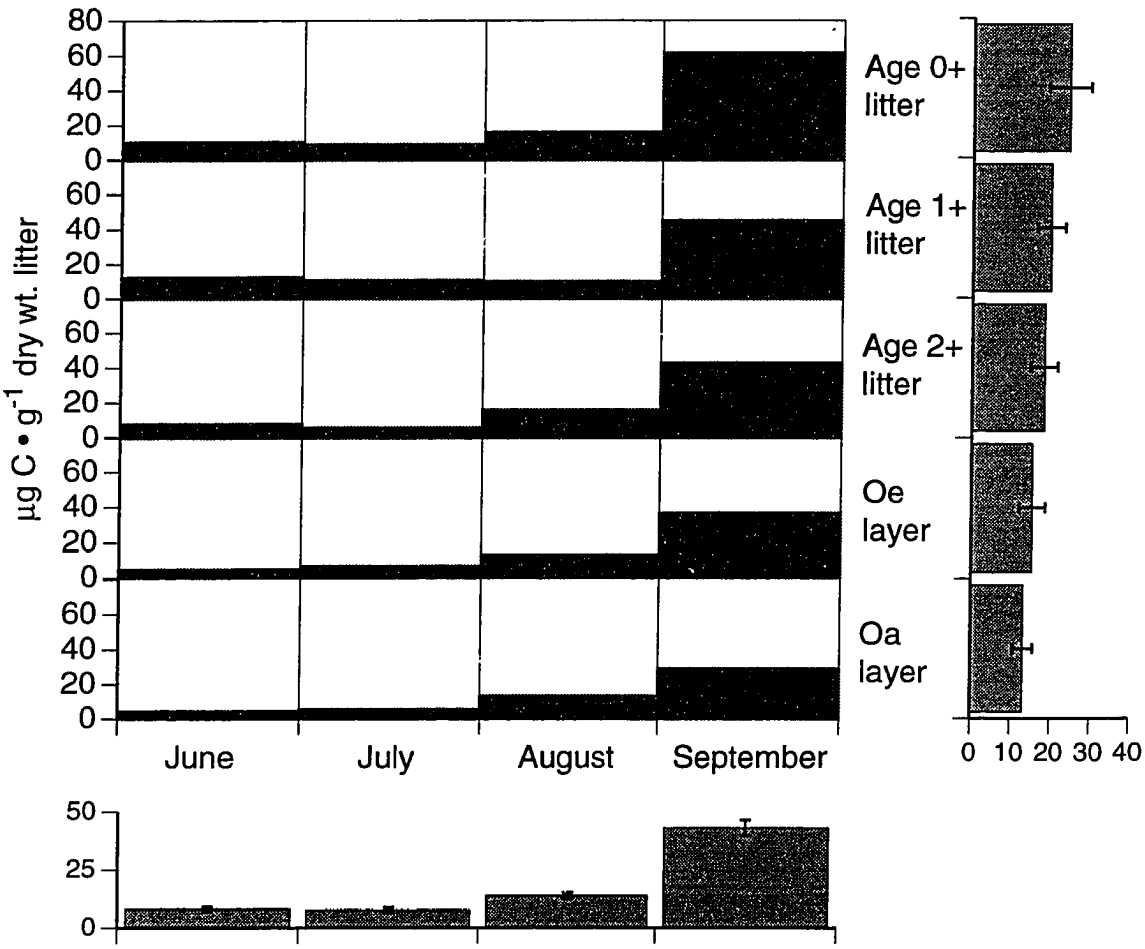

Figure 12. Microbial biomass carbon of forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

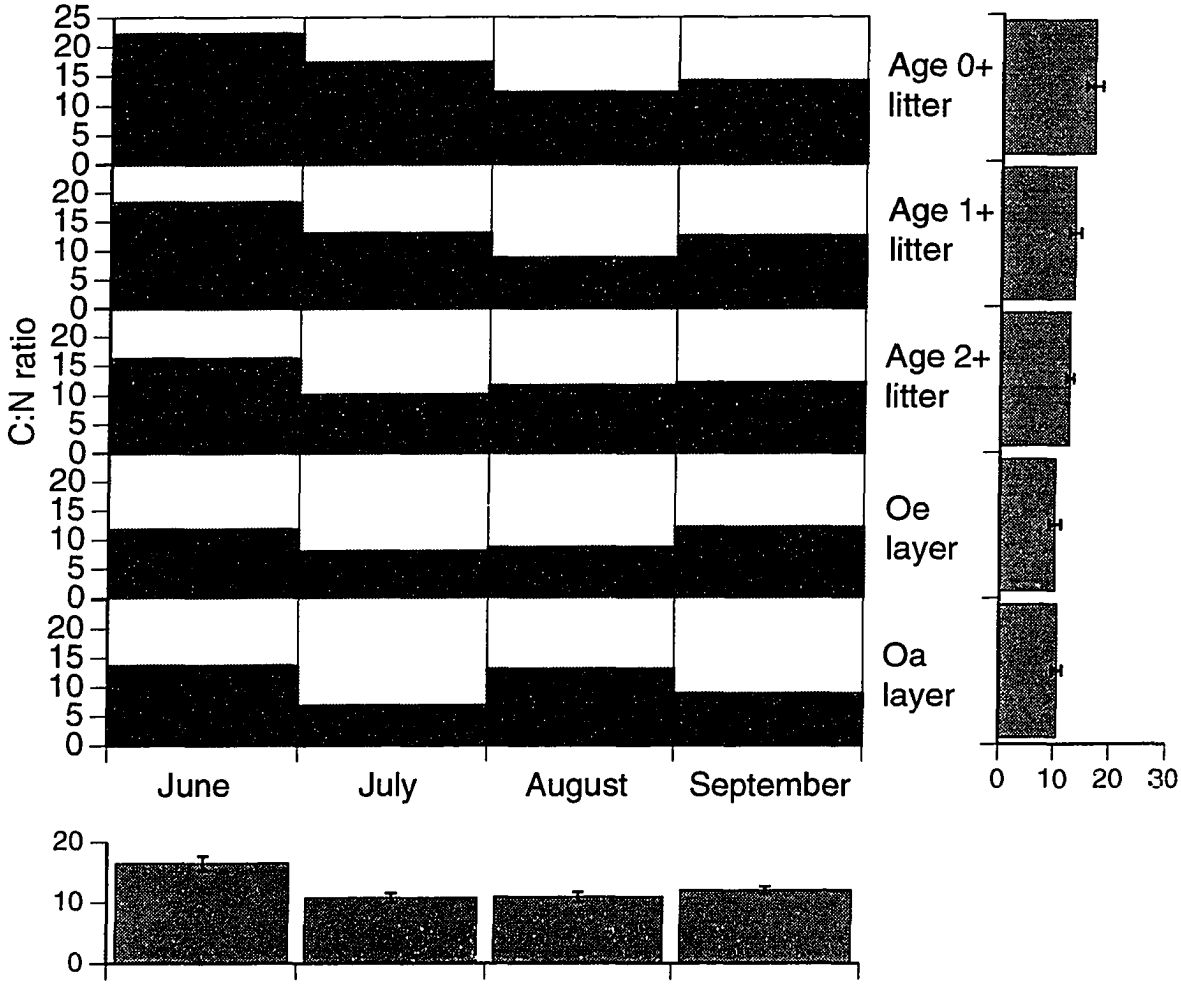

Figure 13. Microbial biomass C:N ratio of forest floor strata, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

nificant ($p \leq 0.01$) overall depth effect. Total fungal biomass (Figure 14*b*) showed a depth effect ($p \leq 0.01$), increasing with depth to a maximum in the Oe layer, and then dropping in the Oa layer. FDA-active fungal biomass was highest in the Age 0+ litter, dropped sharply with depth, and was undetectable in the Oe and Oa layers. Active bacterial biomass (Figure 14*c*) was undetectable in the three upper strata, but present in the Oe and Oa layers ($p = 0.02$). The pattern in total bacterial biomass (Figure 14*d*) was similar to that in the total fungal biomass, with an increase with depth to a high value in the Oe layer and sharp decrease in the Oa layer. The depth effect, however, was not significant ($p = 0.05$).

The environment for decomposition varies with depth down the profile for physical, chemical and biological variables (Figures 7–12). The tethered litter packs placed under the Age 2+ litter lost more mass ($p = 0.02$) and acquired more N ($p \leq 0.01$) than did the litter pack placed under the Age 0+ litter (Figure 15). We also observed that several of the packs placed under the age 2+ litter contained leaves partially skeletonized by the feeding of soil fauna. No such skeletonization was noted in the litter placed under the Age 0+ litter.

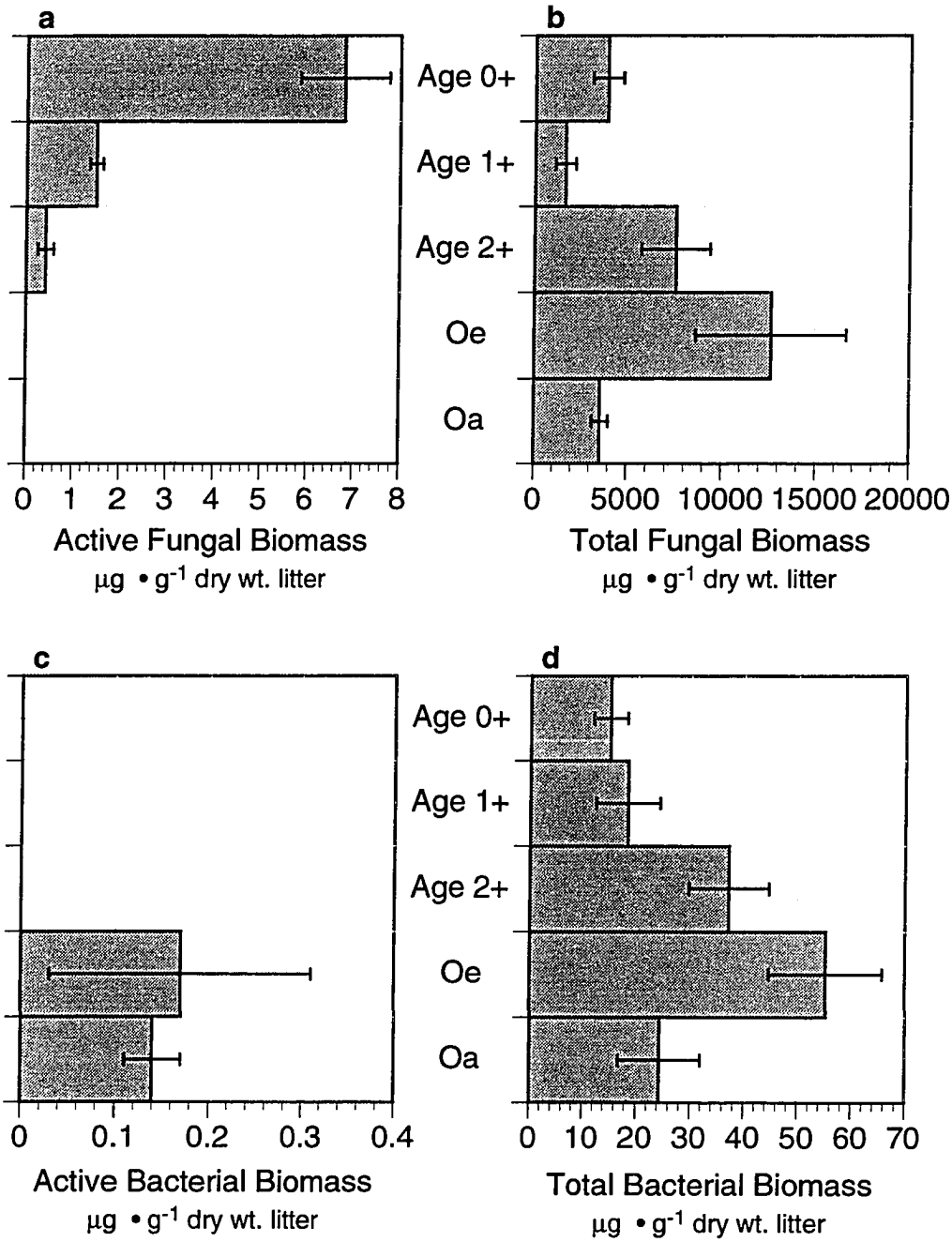

Figure 14. Active and total fungal biomass and active and total bacterial biomass of supplemental samples, September 1993.

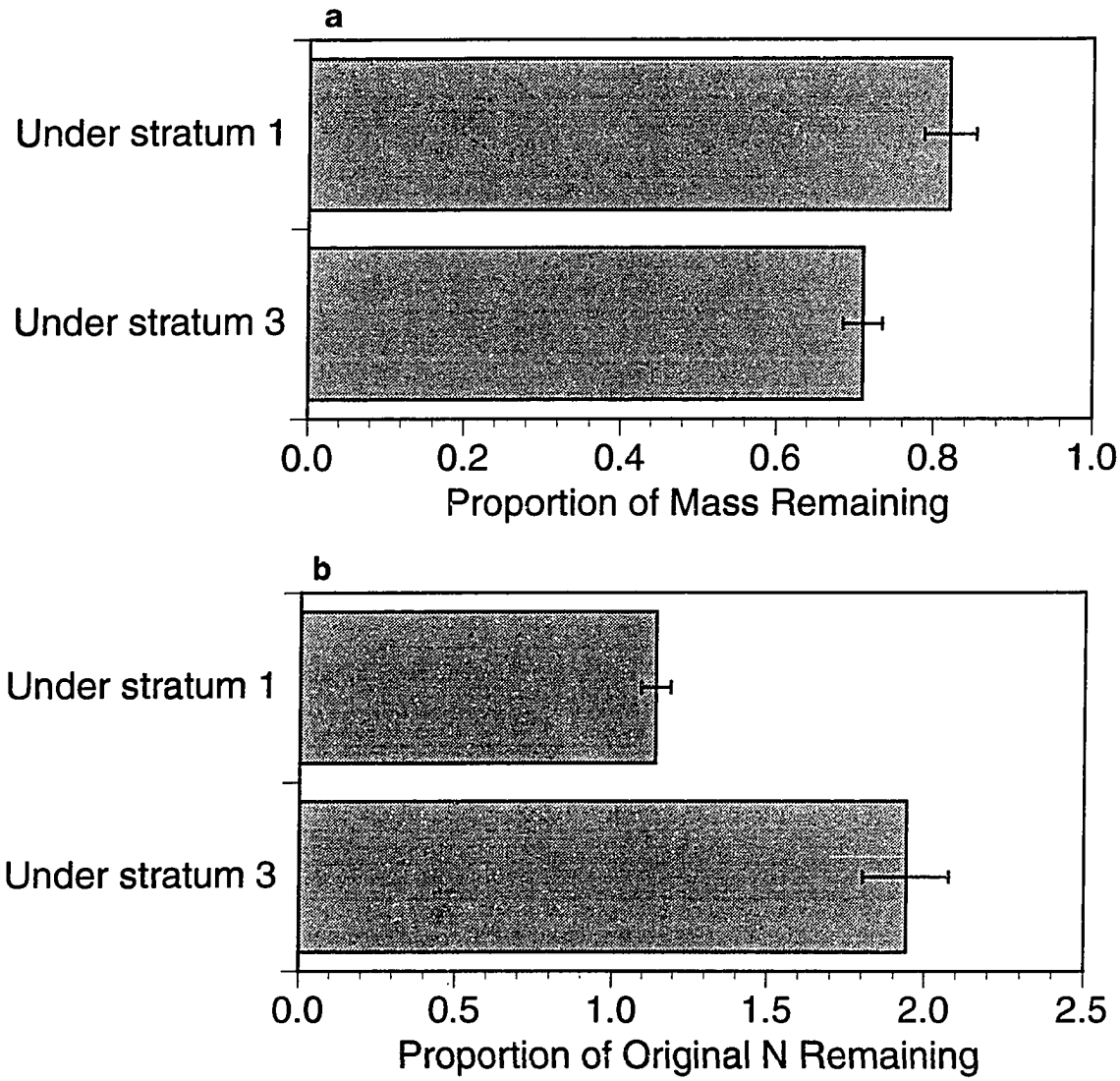

Figure 15. Mass loss and nitrogen immobilization of tethered litter packs placed under the Age 0+ and Age 2+ litter layers for 90 days in summer, 1993.

Discussion

In interior Alaska, paper birch litter has been observed to lose about 21–28% of mass after 1 year on the ground and 34–45% of beginning mass by the end of the 2nd year (Van Cleve, unpublished data). We could not directly calculate rates of litter mass loss from this study—the amount of litter fall varies from year to year—as can be done from litterbag experiments, but we did obtain some information on the residence time of the litter material in the forest floor. Three year-classes of birch litter were easily identified in the forest floor. Below these litter layers, the Oe layer had a turnover rate of about 2 years (calculated by dividing the average mass of material in the Oe layer by the average mass of the Age 2+ layer), assuming steady state. This indicates a five-year residence of leaf litter from the ground's surface to the bottom of the Oe layer. Similar results were reported by Gosz et al. (1973) for yellow birch (*B. allegheniensis*) in a northern hardwood forest in New Hampshire.

C and N dynamics

Paper birch leaves typically contain 48–49% C (by dry weight) when they fall from the tree in mid-September (Wagener and Schimel, in prep.). Much of this carbon is labile and readily metabolized by microorganisms. As decomposition progresses, labile C is mineralized, leaving an increasing proportion of recalcitrant C—lignified material (Flanagan and Van Cleve 1983, and Berg 1991) and microbial secondary products. In most systems, %C does not change with decomposition. Here it seems that silica from *Equisetum* may dilute the organic matter as C is respired away.

The reduction in C:N over time in the decomposing litter is partially because of C loss. This reduction is due also to an accumulation of N in the fresh litter (Gosz et al. 1973, McClaugherty et al. 1985, Melillo et al. 1989). The fresh litter has a deficit in N available for microbial growth, which is alleviated by fungal translocation from zones of net N mineralization deeper in the soil (Ausmus et al. 1976,

Berg and McClaugherty 1989, Hart and Firestone 1991). As the litter ages and the labile C is exhausted the microbes eventually become C limited and start reminer-alizing N. In this birch forest, the shift from N limitation to C limitation and the initiation of net mineralization occurred in the Age 2+ litter. From this stratum and below, N is available for both root uptake and fungal translocation.

Birch leaves at our site continued immobilizing N far longer (in chronological time) than observed in temperate forests (Gosz et al. 1973). This may be because of the short snow-free season and the lower rates of microbial activity under the snow of winter. Net N mineralization appeared to require the overall C:N ratio to drop to 25:1, which is a common threshold value (Gosz et al. 1973, Foster 1989). Below the 25:1 threshold mineralization was possible, but not inevitable (Figure 16). Interestingly, the strongest immobilization also occurred at C:N ratios below 25:1. Overall C:N ratio was not a simple predictor of litter N availability; available N may be limiting to microbial growth even when the bulk C:N ratio is low. The shift from N to C limitation is illustrated by the ratio of C to N mineralized (with negative values disregarded) during the N mineralization assays, which averaged 11.62 in the Age 0+ litter (in which net immobilization was the norm), 470.76 in the Age 1+ litter, 0.47 in the Age 2+ litter, 2.26 in the Oe layer, and 0.19 in the Oa layer. Net immobilization or high ratios of C:N mineralized indicate an N-limited microbial population.

In our data, the overall pattern of increasing net N mineralization with depth is clear, but the pattern over time is less clear (Figure 11). Although differences between months were significant, there was no clear pattern. The highest N immobilization values were in the upper litter strata in September 1993, when the litter was most moist. A correlation of N mineralization with litter moisture was reported by Federer (1983), who noted that litter immobilized N when moist, whereas the same litter mineralized N when dry. We observed that in all strata, mineralization peaked in August just as the forest floor was beginning to rewet after a dry, early summer. This spike in N mineralization may be a result of the

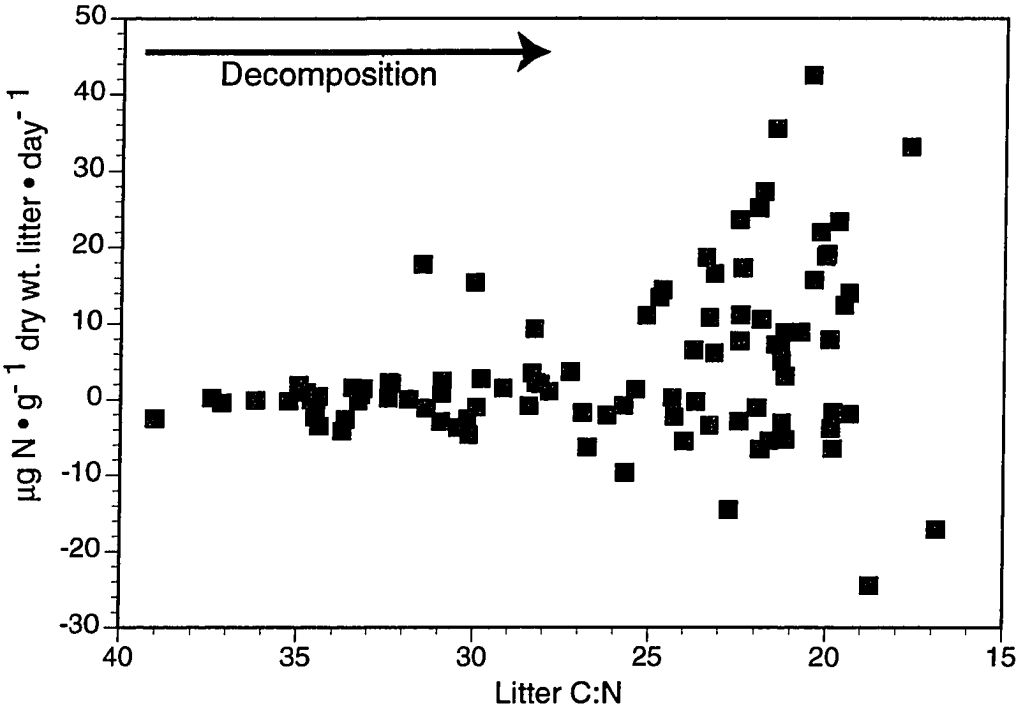

Figure 16. Change in nitrogen mineralization potential as the litter C:N ratio decreases with decomposition. The 1993 data from all strata is included in the plot.

death of microbes on the litter after rewetting (Clein and Schimel 1994). The pulse of immobilization in September is probably associated with regrowth of the microbial population (Figure 11).

The pattern of litter carbon and nitrogen flux is also reflected in litter C:N ratios (Figure 9). There is a long-term decrease in C:N ratio as litter decomposes over the years, as well as a short-term decrease in the newer litter over the course of summer, a pattern documented by others (Gosz et al. 1973). A large incremental decrease appeared in the Age 0+ and 1+ litter layers in September 1993 (Figure 9). This was probably because of a pulse in microbial activity involving both C mineralization and N immobilization as indicated by an increase in microbial biomass, microbial C:N ratio and net N immobilization.

Population dynamics

Although not quantified in this study, live fine roots and associated ectomycorrhizae were observed in the Age 2+ litter and in the Oe layers. The appearance of roots in the Oe layer is not surprising because this is the zone where net mineralization begins (Figure 7*c* and Figure 11). Fewer live fine roots were observed in the Oa layer. As previously noted, the retention time of the material in the Oe layer was approximately 2 years. The transit time, then, to the Oa layer for roots first appearing in the Age 2+ litter would be 2–3 years. The turnover rate of fine birch roots in upland taiga is 33% per year (Ruess, et al., in review). Thus the Oa layer may be a graveyard for spent roots first growing in the litter layers.

The C:N ratio in the litter might be expected to influence the nutrient status of decomposer microbes. Less C is available to microbes as litter carbon becomes more recalcitrant. Like litter C:N (Figure 9), the biomass C:N ratio (Figure 13) decreased between June and August. Unlike litter C:N, biomass C:N increased in September. The increase of biomass C:N in September might be explained in two ways. There may have been an input of labile carbon or the composition of the microbial community might have changed, or both.

Where might extra labile C be coming from? In early September, relatively high precipitation corresponds with leaf senescence. Throughfall containing labile C leached from senescing leaves may be priming the microbial biomass. The litter C:N ratio, however, decreased in September. Might any labile C input to increase litter C:N? The microbial biomass C of the top litter layer in September is only about 25 mg C per gram of litter C. Microbial uptake of labile C from throughfall therefore might affect microbial nutrient balance without changing total litter C.

The second possibility is a change in microbial community composition. Fungi characteristically have higher C:N ratios than do bacteria. C:N ratios for litter fungi are ≥10–12:1, whereas bacteria range from 4–6:1 (Tate 1995). If the biomass of fungi were to increase relative to bacteria, the overall microbial C:N ratio would also increase. We observed a big increase in the sulfate-extractable microbial biomass in September 1993 and direct counts for that month showed nearly 100 times more fungal than bacterial biomass in the forest floor material. August is also a period of active fungal fruiting, suggesting intense fungal activity. We do not know, however, from this study how the ratio of fungal to bacterial biomass might have changed over the course of summer.

In forest soils, fungi usually dominate the microbial biomass (Parkinson 1988). Direct counts of FDA-active fungi register only the active growing tips of the hyphae and probably therefore underestimated actual live fungal biomass. Metabolically-active fungal biomass typically makes up only a small part of total fungal biomass (Söderström 1979, Berg 1991). Fungi can allocate protoplasm to hyphae where resources are available. The restriction of active fungal biomass to the upper strata, in September at least, is likely a response to the availability of labile C. The lack of FDA-active fungi at depth does not indicate a lack of live fungi.

The decomposition of birch litter cohorts can be viewed as an incremental conveyor of organic matter into the forest floor. Fresh litter enters the system in autumn, remains on the surface (as the age 0+ litter) for 1 year, and then becomes

the age 1+ litter the next autumn. After a year as the age 1+ litter and another as the age 2+ litter, the litter is "dumped" into the Oe layer, where it is subject to consumption by larval dipterans and perhaps mixed by the movements of these dipterans and enchytraeid worms (Wagener et al., in prep.). Fungi colonize the fresh litter at the surface and the fungal biomass rides the conveyor down the profile for the first few years, perhaps explaining the presence of active hyphae in the surface, but the greater total hyphae at depth. The fungi are thus in place both to exploit labile C and to take up N as it becomes available. As the litter passes along the conveyor it loses labile C and at first gains and later loses N. The quality of the litter when it falls to the ground influences the timing along the conveyor of N release (Wagener and Schimel, in prep). A portion of the released N is pumped back to the start of the conveyor by fungi to fertilize fresh litter. Another portion is siphoned off by root-mycorrhizal assemblages. Within each yearly increment along this conceptual conveyer, the litter is affected by seasonal cycles in climate and microbial biomass (Moore 1985, Berg 1991). When moisture and microbial biomass are high, microbial transformations of the litter are accelerated.

As litter passes between yearly increments on the conveyor—becomes older and deeper in the forest floor—the decompositional environment also changes. Changes in the status of litter and in the micro-environment are separate effects, but they co-vary. The seasonal cycles described above become less pronounced with depth. The microclimate is moister and less variable and microbes have a decreased likelihood of water stress.

The view of decomposition presented by litter bag experiments—the loss of mass and the release of nutrients from decomposing leaf litter over time— suggests a linear process. The quality of litter as a substrate for microbes and the physical texture of the material generally may change unidirectionally. But even litter quality is under the influence of cyclical events. The forest floor is flushed with dissolved organic matter every spring with snowmelt and perhaps in early autumn as well. During the snow-free period, substrate availability can be

affected by any compounds leaching from the litter above. The microbes also are under the constraint of trophic interactions (e.g., grazing by protozoa and micrometazoans).

Although decomposition of leaf litter is rightly seen as a continuum from leaf to humus (Ågren and Bosatta 1987, Melillo et al. 1989, Rustad 1994), the separate physical, chemical, and biological environments in which decomposition takes place cannot themselves be considered simple continua. A spiral might a useful metaphor for an overall pattern in the decompositional environment over time within the forest floor system: a directional change in state coupled with a cyclical (seasonal) change in environment.

Our hypothesis—microbial activity on a particular litter cohort is a controlled primarily by litter quality, but is modified by the vertical position in the forest floor and seasonal climatic variation—was supported by several lines of evidence. At this site, N content of birch litter may vary greatly from year to year. The content of N at the beginning of decomposition strongly influenced the timing and extent of N release from that litter (Wagener and Schimel, in prep.). The influence of initial quality may only last for the first few years of decomposition, but during this time fungal biomass is active and decomposition is N limited. As fungi move N from sites of availability to sites of demand, N demand of one cohort of litter might influence N availability for other cohorts. The microbial activity on a particular litter cohort in the forest floor would then be influenced not only by its own quality, but also by the quality of adjacent cohorts. These dynamics of N availability and demand by microbes must also affect N available for root uptake.

Data from the field incubations of tethered litter established that the decompositional environment varies with depth in the forest floor. Quality of the environment for microbial activity on a litter cohort increases incrementally over time. These data also make clear that macroclimatic cycles control microbial biomass. We believe then that microbial processes on a particular cohort are controlled by

litter quality, vertical location, and seasonality of weather and that these variables interact to bring about the complex outcomes we observed.

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Stratification of soil fauna distribution in space and time in the birch forest floor

The forest floor is a setting for decomposition, where nutrients are released from plant detritus and made available for plant uptake, and where C is stored and respired to the atmosphere. In the forest floor, the macroscale variables that drive processes at a landscape-scale influence the microscale variables that regulate activity of decomposer microbes and the faunal food webs based on them.

The decomposing detritus making up the forest floor serves simultaneously as an ever-changing substrate and habitat for soil flora and fauna. Patterns of microclimate in the forest floor, its suitability as habitat, and the availability of food constrain the distribution and movements of soil fauna (reviewed by Luxton 1981). The soil fauna may, in turn, modify their habitat and food availability through their feeding activities. If they are active in litter comminution—reducing large pieces of leaf litter to small pieces—they will affect the water holding capacity of detritus and thus the environmental conditions in which the fauna live.

The taiga forest floor is a stratified environment. In mid-successional hardwood stands the forest floor consists of distinct litter layers at different decompositional stages atop a thick layer of fine particulates and dead roots. The forest floor is also stratified in time by a highly seasonal climate.

To relate biotic processes to the chemistry of the litter substrate, to the microclimatic conditions at that particular point in the forest floor, and to the status of the organisms responsible for the process, requires a high spatial resolution. The classic litter– fermentation–humus horizon (Oi—Oe—Oa) designations employed by many others (Van Cleve and Sprague 1971, De Boois 1974, Quesnel and Lavkulich 1981, Federer 1983, Flanagan and Van Cleve 1983, Salonius 1983, Kögel 1986), although otherwise useful, have limitations in this regard. The Oi horizon typically contains litter from more than one yearly leaf crop, and a study of the Oi as a

whole necessarily combines litter of various decompositional ages. During the first few years of decomposition (while litter is combined into the Oi horizon), birch litter undergoes profound change, losing labile C and gaining N. Microbial processes shift from nutrient limitation to C limitation during this time (Wagener and Schimel, in prep.). To better relate faunal distributions to microbial processes on litter, we must distinguish forest floor strata based on yearly leaf crops (cohorts) and examine the dynamics of forest floor organisms in these strata simultaneously across time.

Previously, we presented a method for discriminating yearly cohorts of litter in the birch forest floor and described the dynamics of microbial processes in these cohorts over the brief Alaskan summer (Wagener and Schimel, in prep). This study examines a broad range of faunal taxa occurring in these same five forest floor layers of different decompositional age. The questions we ask are:

1) How do faunal distributions vary over depth and time?
2) How do seasonal patterns of macroclimatically-influenced microclimate constrain faunal distributions? and
3) How do seasonal patterns of microclimatically-influenced microbial biomass affect faunal distributions?

Methods and Materials

This study was conducted at the University of Alaska Arboretum, adjacent to the university campus in Fairbanks, Alaska (64° 51' 36" N, 147° 50' 24" W). The site consists of a near-uniform 100–130-year-old stand of paper birch (*Betula papyrifera*) on the top of a ridge at 144 m elevation. A thick growth of *Equisetum arvense* (horsetail) covers the forest floor. The soil at this site is an alfic cryochrept.

At the arboretum study site, distinct layers of *Equisetum* litter separate the three newest year classes of birch litter in the forest floor. *Equisetum*, because of its texture and the presence of silica in its tissues, leaves a long-lasting residue that provides a sharp visual contrast with birch litter. Because of the absence of macroinvertebrates, litter does not rapidly mix with underlying forest floor material and each birch leaf generally maintains its location relative to surrounding litter for 3 to 4 years.

We sampled the forest floor of the arboretum on 9 September 1992, and 1 June, 5 July, 5 August, and 5 September 1993. At each date, five replicate samples were taken from random locations within a 10 m square grid. Each replicate consisted of five 0.02 m^2 cores that were taken within 3 cm of each other and composited. To take each core, we placed the corer on the forest floor at the random grid point and cut the forest floor around the corer with a serrated-edge knife. We brought the forest floor material into the laboratory and separated it by strata.

Equisetum litter served as the marker separating the three most recent year-classes of birch litter (the age 0+, 1+, and 2+ litter). Below the age 2+ litter, the Oe layer consisted of the distinct layer of material made up of leaf parts. Below this was a sharp transition into a zone of fibrous material with few, if any, recognizable leaf parts. The upper 5 cm of this layer was defined as a subsample of the Oa layer. Material below this was discarded, along with woody debris and course roots from all strata. The entire organic layer—Oi, Oe, and Oa— is 8 to 10 cm

thick. Beneath the organic forest floor is a thick loess layer, which is about 98% inorganic.

We took two weighed subsamples (approximately 2 g each at field moisture) of each stratum of litter for invertebrate extraction. The extraction funnels were constructed from 500 ml polypropylene bottles cut in half. A hardware cloth screen (1 cm mesh) was placed inside the neck of the half containing the lid. The resulting extractors acted as modified Tullgren funnels. A high moisture and temperature gradient was set up in the litter samples using heat lamps above and a refrigerated water bath below a sheet of 2.5 cm thick "blue foam" polystyrene insulation, in which the funnels rested. One subsample of each litter was extracted "dry" suspended above a dish of ethanol (70%) mordant. The other subsample was extracted "wet" with the litter in contact with the surface of water in a dish. The water-filled pore creatures (nematodes, tardigrades, and rotifers), enchytraeid worms, and larval dipterans were more likely to be extracted by the wet technique, whereas microarthropods were obtained from dry extraction.

We kept each litter subsample in the extractors for 3 days. Each of these 3 days the heat lamps were on for 8 hours. At the end of this period, ethanol was added to the dishes as needed, the dishes capped, and the preserved invertebrates stored for subsequent identification. The resulting collection of fauna was from two types of extractions (wet and dry) from five replicates of the five forest floor strata on five sampling dates.

A subset of the samples were examined to determine the distribution of nematode feeding morphologies. All the fauna in 10 wet-extracted samples from each sampling date (two randomly-chosen samples from each of the five strata) were placed on slides. Starting with the top left corner of the cover slip, each slide was examined under a compound microscope in a set of transects across the area of the cover slip. The first 50 nematodes (when present) were examined. Nematodes were categorized into one of three feeding-modes, based on mouth anatomy (Freckman and Baldwin 1990). Nematodes (Tylenchida and some Dorylaimida)

having a protrusible hollow stylet are typically phytophagous or fungivorous, although some are predatory or parasitic. Nematodes (Mononchida) with a cuticularized stoma and at least one large tooth were classified as predators. The remainder of the nematodes had open, unarmed stoma and were probably microbivorous, although many also likely feed on small protozoa and fungi. These we classified as microbivorous-omnivorous.

Litter-comminuting fauna, such as earthworms, isopods, and millipedes, are absent from interior Alaska. We have, however, observed the larvae of some locally occurring dipterans consuming birch leaves in the laboratory. To confirm the comminution of litter by dipteran larvae in the field, gut contents were examined in another subset of 10 samples per sampling date. The fore- and midgut of five individuals (when present) of each dipteran family from each sample were dissected and the contents spread on slides. The types of food items were estimated as a proportion of total gut contents.

Statistical analysis consisted of one-way and two-way analysis of variance (ANOVA). In the one-way ANOVAs, post-hoc tests were conducted using the Scheffé test statistic, and in the two-way ANOVAs, cell-to-cell comparisons were conducted as contrasts within the general linear model. Data used in the ANOVAs were first rank-transformed (Conover and Iman 1981), to compensate for non-normality. Data were analyzed using Systat software (version 5.2).

Results

In data presented here, the time scale is expressed in two ways. Within-year time is shown as the month-to-month changes in faunal abundance of the forest floor material. Between-year time steps are seen in the differences between the year-classes of litter comprising the forest floor strata. In the bar graphs of the September 1992 data (Figure 17), between-year time (depth) is displayed on the vertical axis. In the graphic matrices of the 1993 data (such as Figure 18), within-season time is displayed along the overall horizontal axis of each figure, whereas between-season time is depicted on the overall vertical axis. In presenting the results of the ANOVAs, within-season time will be referred to as the "time" effect and between-season time—comparisons between strata—will be referred to as the "depth" effect. All abundances of organism are expressed as numbers per gram dry weight of litter.

The water-filled pore creatures

In September 1992 (Figure 17*a*), the distribution of nematodes—considered all together—varied with depth ($p \leq 0.01$). The highest abundance was in the age 2+ litter and the lowest in the Oa layer. The abundance of nematodes in 1993 (Figure 18) showed both time ($p \leq 0.01$) and depth ($p \leq 0.01$) effects. The interaction was also significant ($p \leq 0.01$). Overall, the mode of the vertical distribution of nematodes was in the age 2+ litter and the lowest abundance was in the Oa layer. Abundances in the age 2+ litter and the Oe layer decrease from June through August and the top four strata all increased in September (Figure 18). In these layers the fewest nematodes occurred in August.

The numbers of stylet-bearing (phytophagous and fungivorous) nematodes generally increased over summer ($p \leq 0.01$, Figure 19) and showed a depth effect ($p \leq 0.01$), with average abundance greatest in the age 2+ litter. The stylet-bearing nematodes also exhibited a significant time-depth interaction ($p \leq 0.01$). Predaceous nematodes generally varied over summer ($p \leq 0.01$, Figure 20), but showed

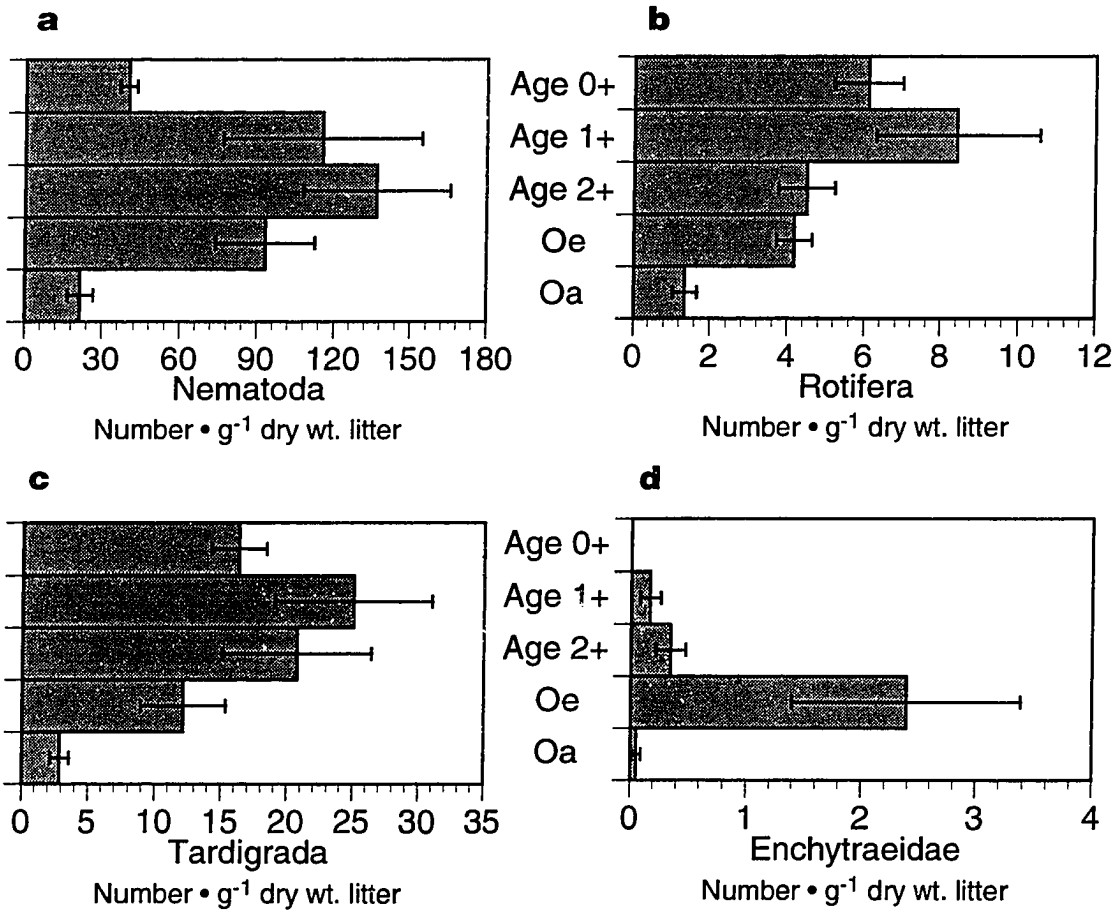

Figure 17. Distribution of Nematoda, Tardigrada, Rotifera, and Enchytraeidae (Oligochaeta) in the forest floor strata, September 1992.

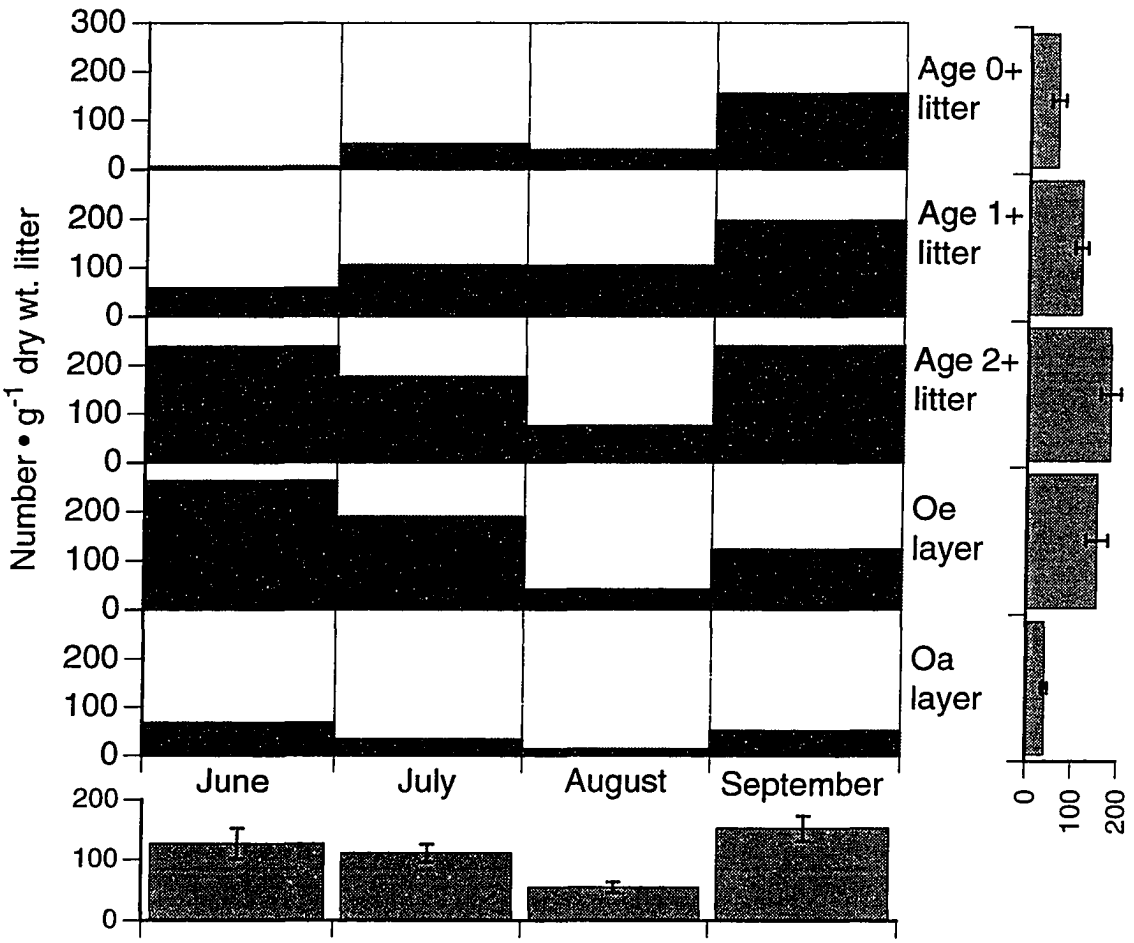

Figure 18. Distribution of Nematoda in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

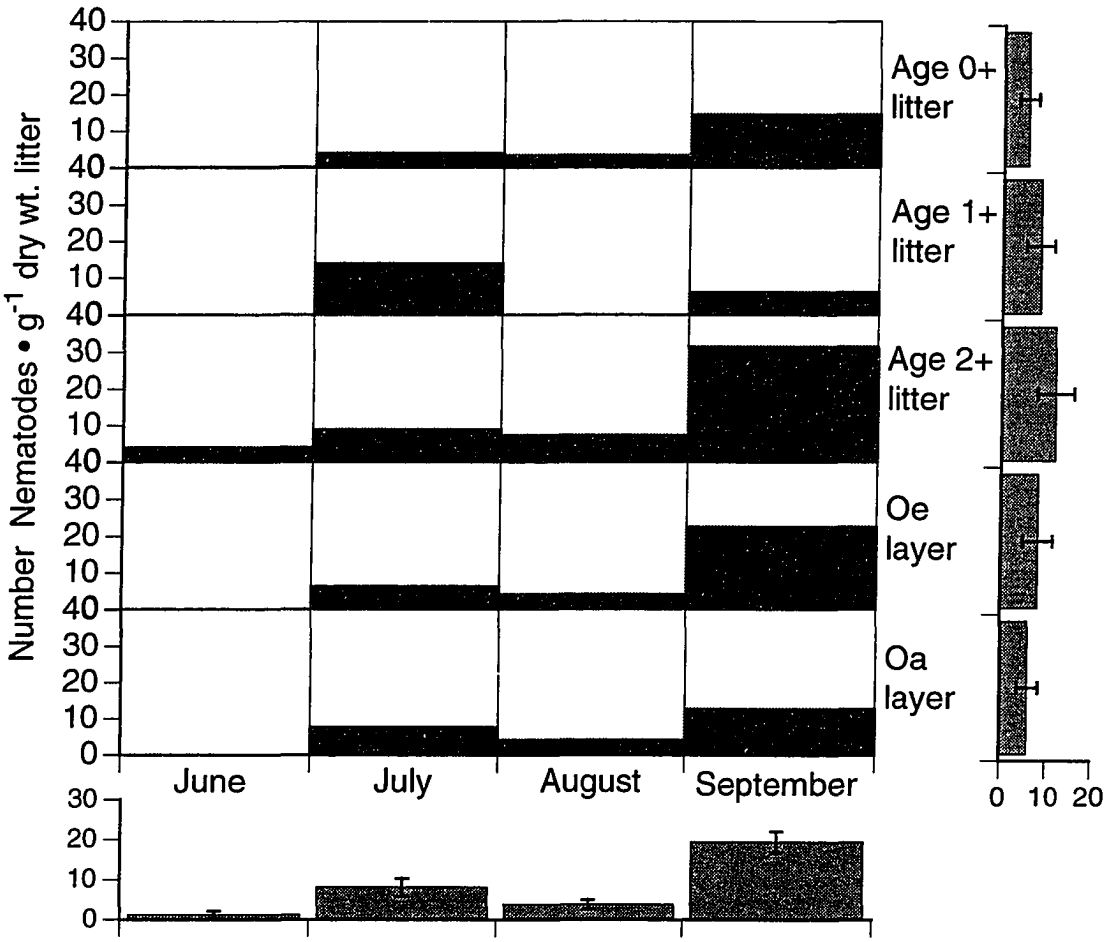

Figure 19. Distribution of stylet-bearing nematodes, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

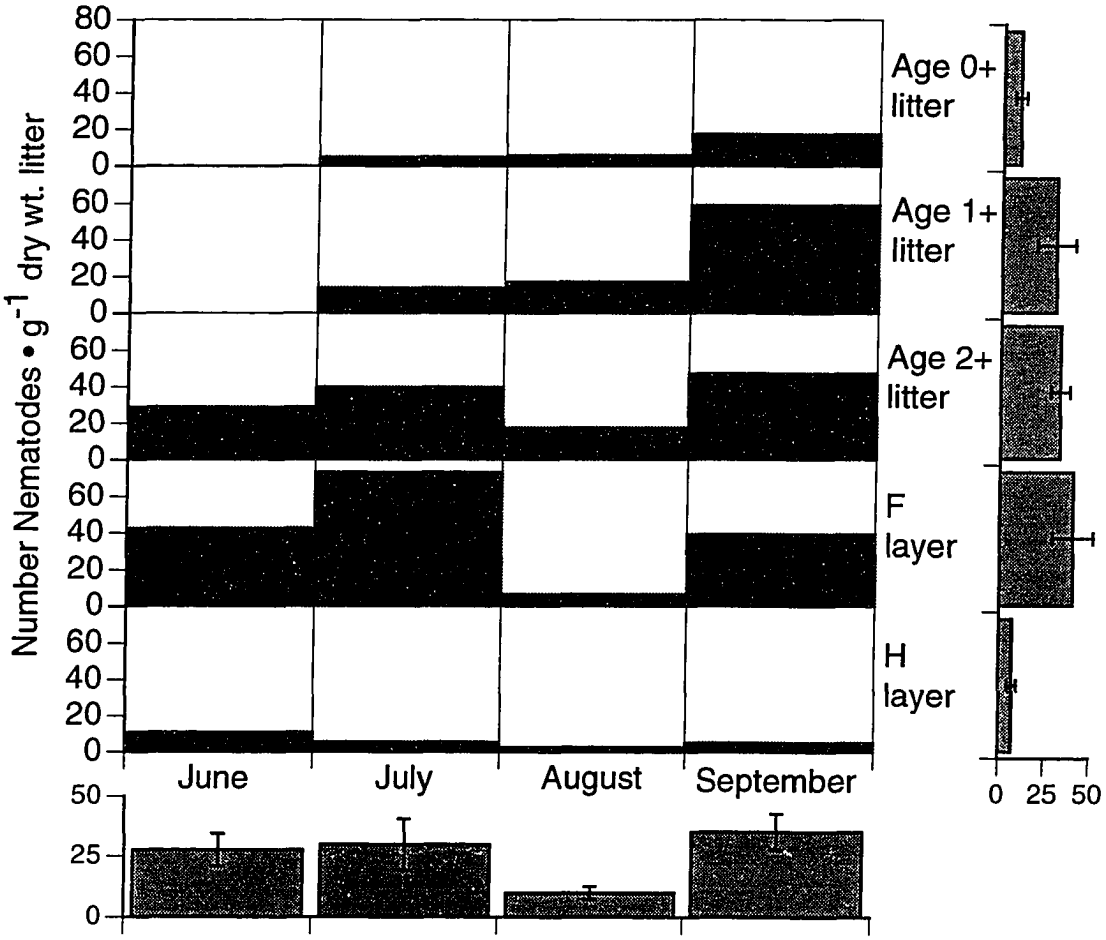

Figure 20. Distribution of predaceous nematodes, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

no overall depth effect or time-depth interaction. Microbivores-omnivorous nematodes showed a significant depth effect ($p \leq 0.01$, Figure 21), with overall distributions centered in the age 2+ litter, and a time-depth interaction ($p \leq 0.01$), but no change over time.

Rotifer distribution in September 1992 (Figure 17*b*) varied significantly with depth ($p \leq 0.01$). Rotifers were highest in abundance in the age 1+ litter and lowest in the Oa layer. The distribution of rotifers in 1993 (Figure 22) showed a depth ($p \leq 0.01$) effect, but no significant time effect; the interaction effect was significant ($p \leq 0.01$). Overall, the highest abundances of rotifers occurred in the age 2+ litter and the Oe layer and the lowest in the Oa layer.

In September 1992 (Figure 17*c*), the distribution of tardigrades varied with depth ($p \leq 0.01$), with the highest numbers in the age 1+ litter and the lowest in the Oa layer. In 1993, the distribution of tardigrades (Figure 23) showed a depth effect ($p \leq 0.01$), a time effect ($p \leq 0.01$), but no significant interaction. In June the highest numbers of tardigrades occurred in the age 2+ litter and in September, in the age 1+ litter.

The enchytraeid worm distribution in September 1992 (Figure 17d) varied ($p \leq 0.01$) with depth. The highest abundances were in the Oe layer and no worms occurred in the age 0+ litter. In 1993 (Figure 24), there was a depth effect ($p = 0.06$), but no significant time effects or interaction occurred. The overall pattern of enchytraeid abundance in 1993 was similar to September 1992. No worms occurred in the age 0+ litter and the greatest abundance of enchytraeids occurred in the Oe layer.

Arthropods

In September 1992, there was no significant depth effect in the distribution of mesostigmatid mites (Figure 25*a*). In 1993, mesostigmatid distribution (Figure 26) varied with depth ($p = 0.04$), but not over time. The interaction term was signifi-

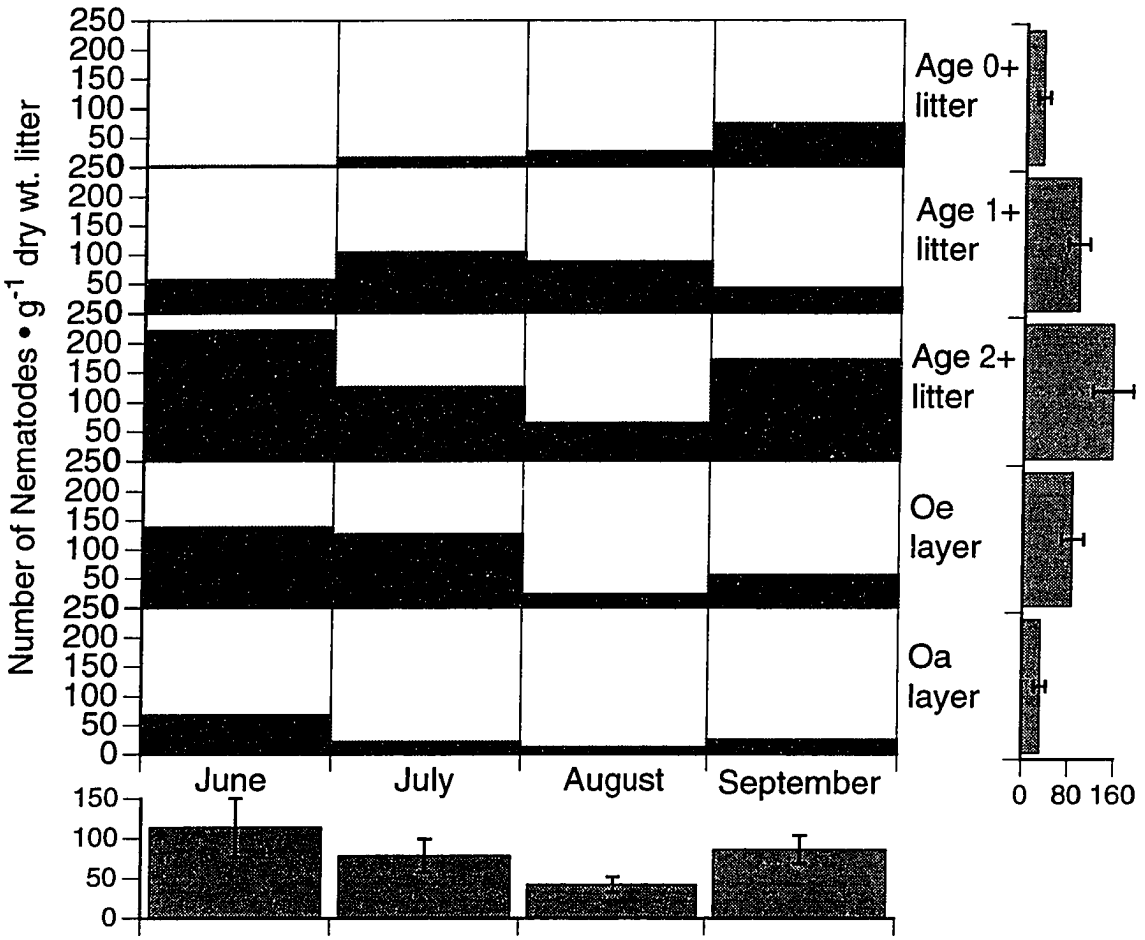

Figure 21. Distribution of microbivorous-omnivorous nematodes, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

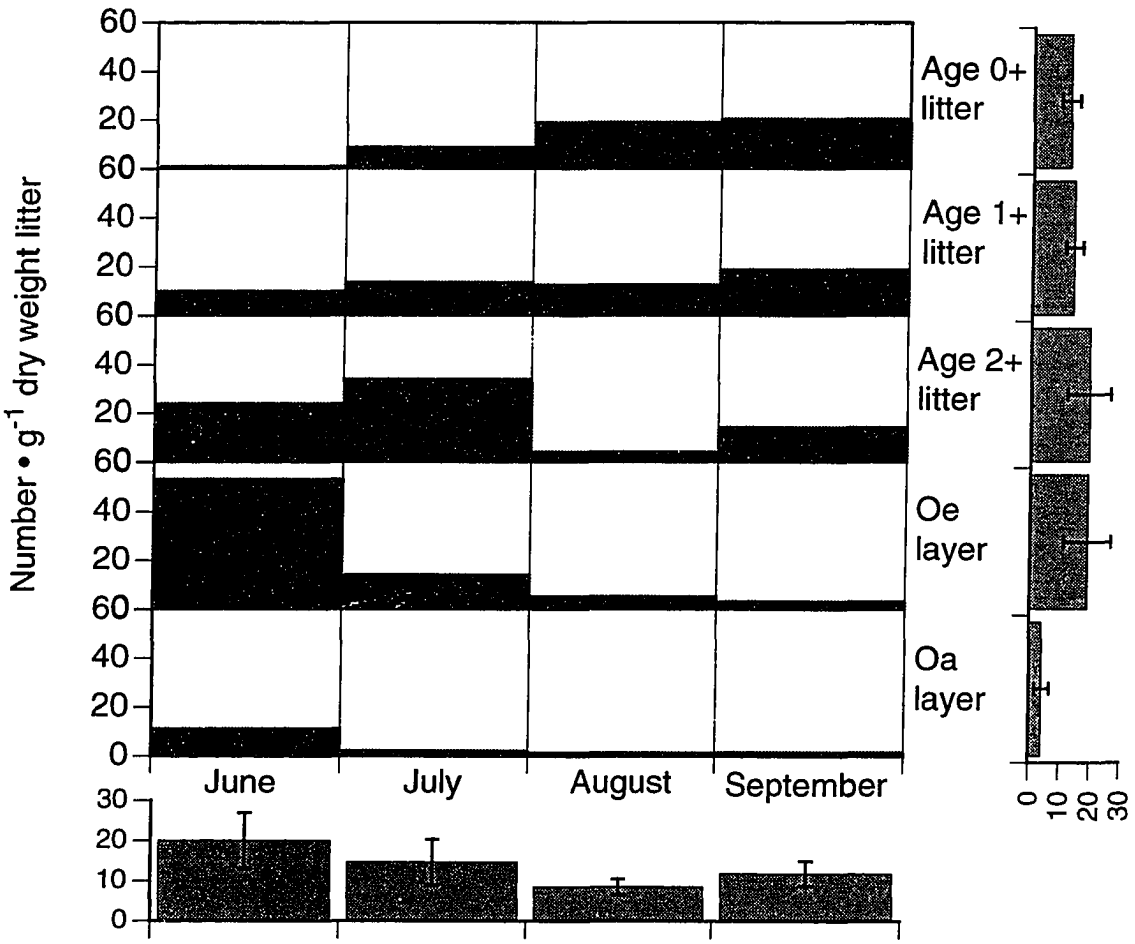

Figure 22. Distribution of Rotifera in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

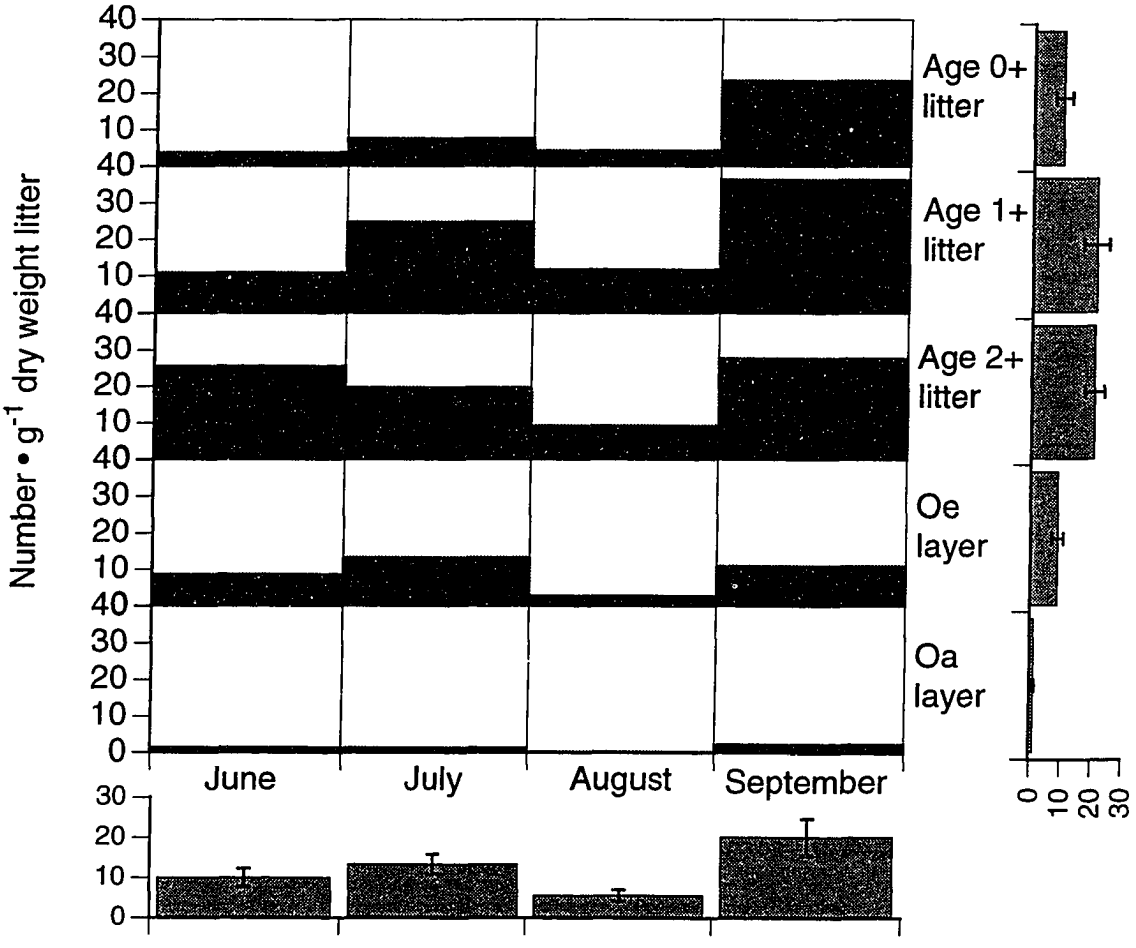

Figure 23. Distribution of Tardigrada in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

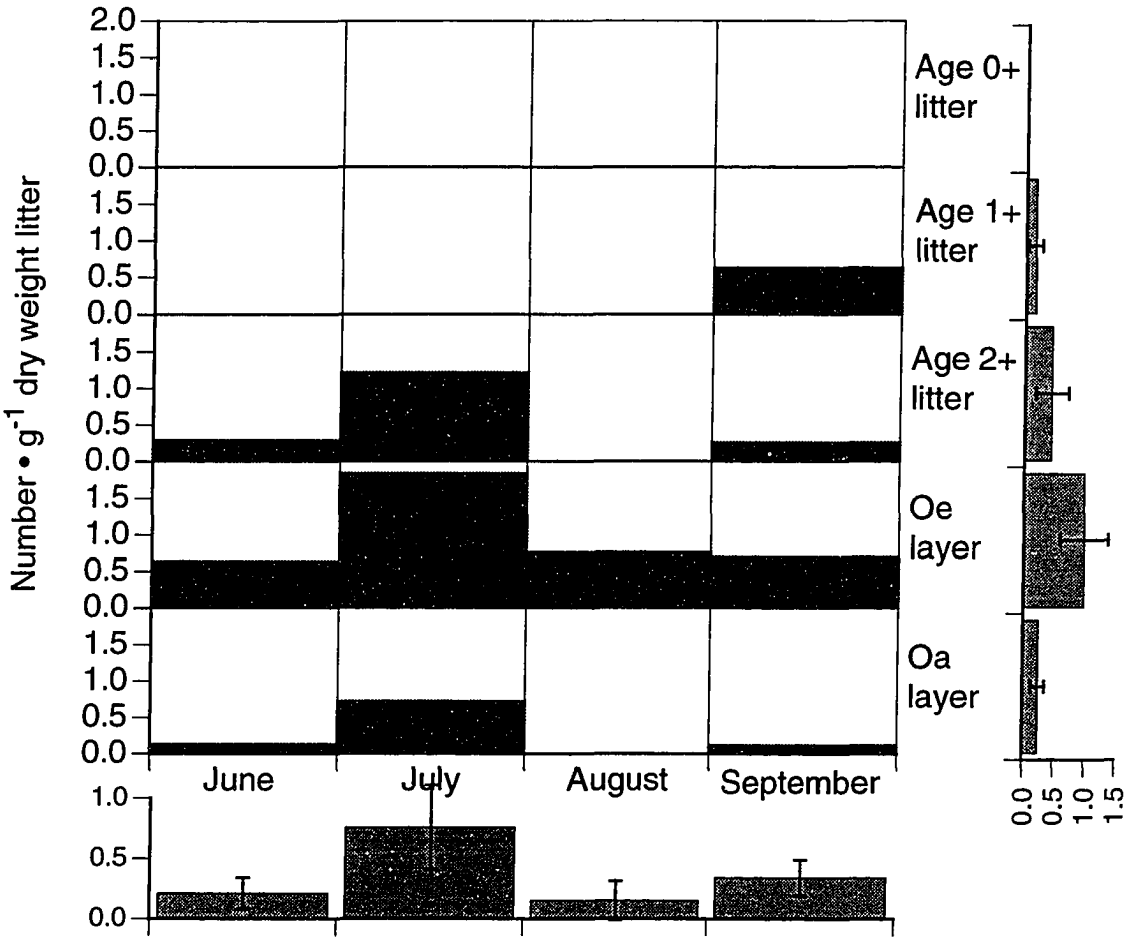

Figure 24. Distribution of Enchytraeidae (Oligochaeta) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

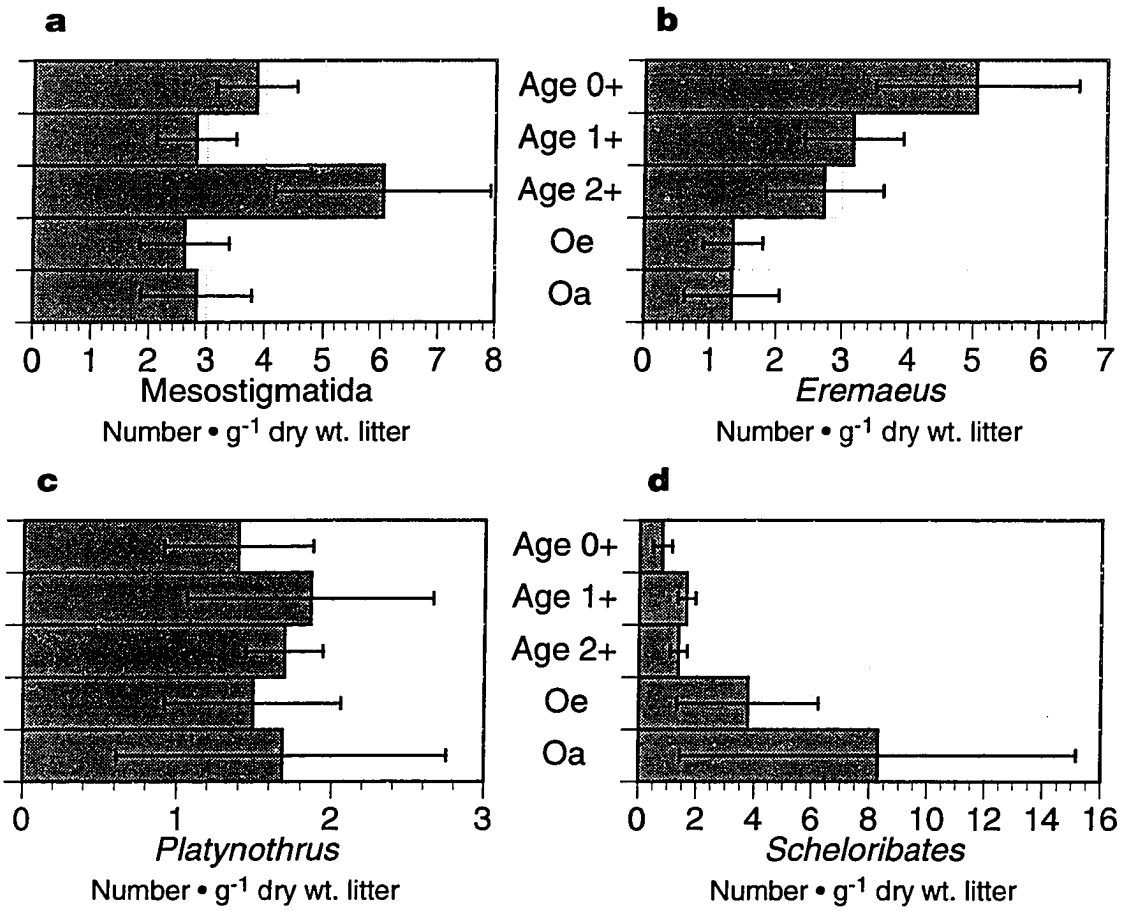

Figure 25. Distribution of Mesostigmatida and three genera of oribatids in the forest floor strata, September 1992.

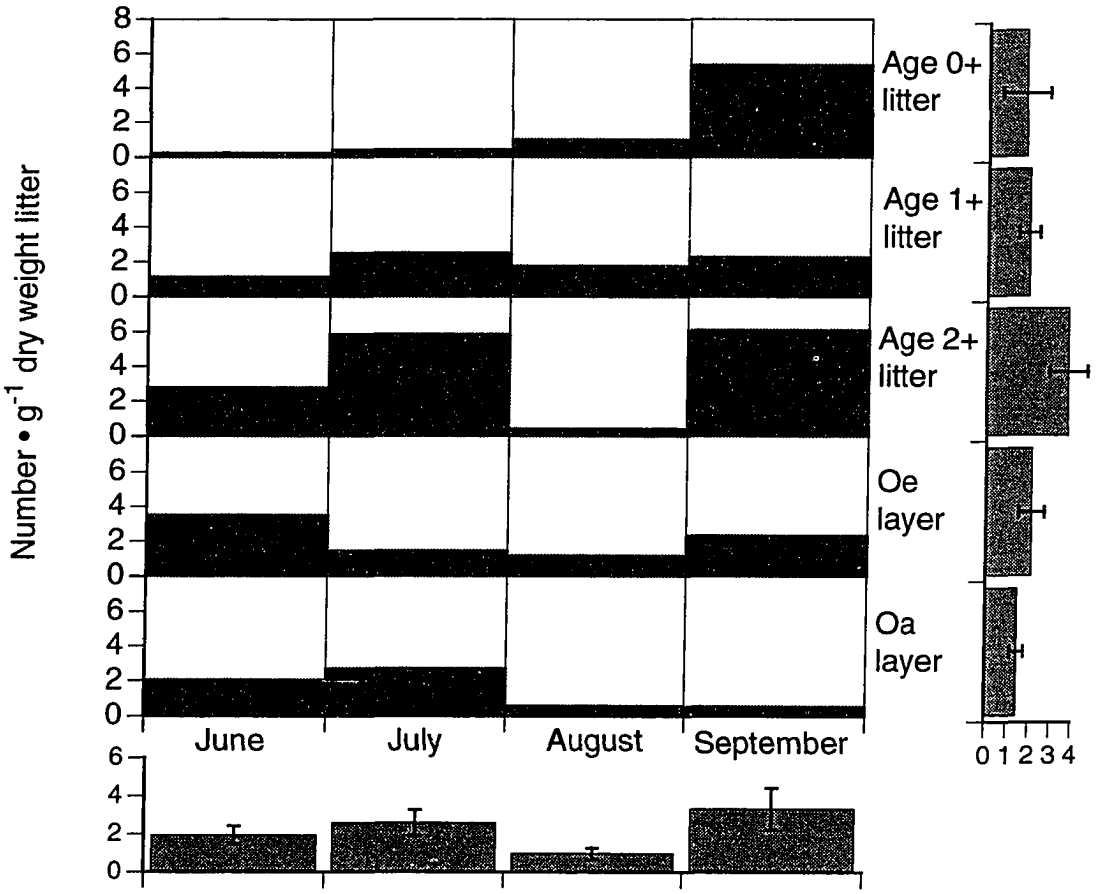

Figure 26. Distribution of Mesostigmatida (Acarina) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

cant ($p = 0.04$). Over summer, the highest abundances of mesostigmatids mites were in the age 2+ litter.

Of the three most common genera of oribatid mites (Figure 25*bcd*), *Eremaeus*, *Platynothrus*, and *Scheloribates*, none showed a depth effect in September 1992, although *Eremaeus* appeared to decrease and *Scheloribates* appeared to increase with depth. Only *Eremaeus* (Figure 27) and *Platynothrus* (Figure 28) varied with depth in 1993. Overall *Eremaeus* were equally numerous in the top four strata and less numerous in the Oa layer ($p = 0.07$). *Platynothrus* overall were most abundant in the age 2+ litter and least in the Oa layer ($p = 0.03$). Abundances of *Platynothrus* ($p = 0.09$) and *Scheloribates* ($p = 0.06$, Figure 29) generally decreased over the summer, while *Eremaeus* showed no significant time effect, although these mites appeared to increase in abundance over the summer. None of these genera showed significant interactions between depth and time.

In September 1992, abundances of collembolans in the family Entomobryidae ($p = 0.01$) decreased and Onychiuridae ($p \leq 0.01$,) increased with depth (Figure 30ac). Although Isotomidae (Figure 30b) showed no significant depth effect, the largest numbers occurred in the Oe layer.

In 1993, Entomobryidae (Figure 31) showed a depth effect ($p = 0.01$), were most abundant in the age 1+ and 2+ litter, occurring in the Oe layer only in June, in the age 0+ litter only in September, and not at all in the Oa layer. The time effect and interaction were not significant. Isotomidae (Figure 32) exhibited time ($p = 0.02$) and depth ($p = 0.06$) effects, but no interaction. The numbers of isotomids increased with depth, although none occurred in the age 0+ litter. Isotomids were most abundant in June and least in August. Onychiuridae (Figure 33) showed a time effect ($p = 0.06$), but no depth effect or interaction. Onychiurids were most numerous in June and least numerous in August.

Gut contents of larvae of the most common dipteran families is summarized in Table 4. A large portion of the gut contents of Chironomidae and Mycetophilidae consisted of roots and leaf parts. Because these litter-eating larvae occurred in

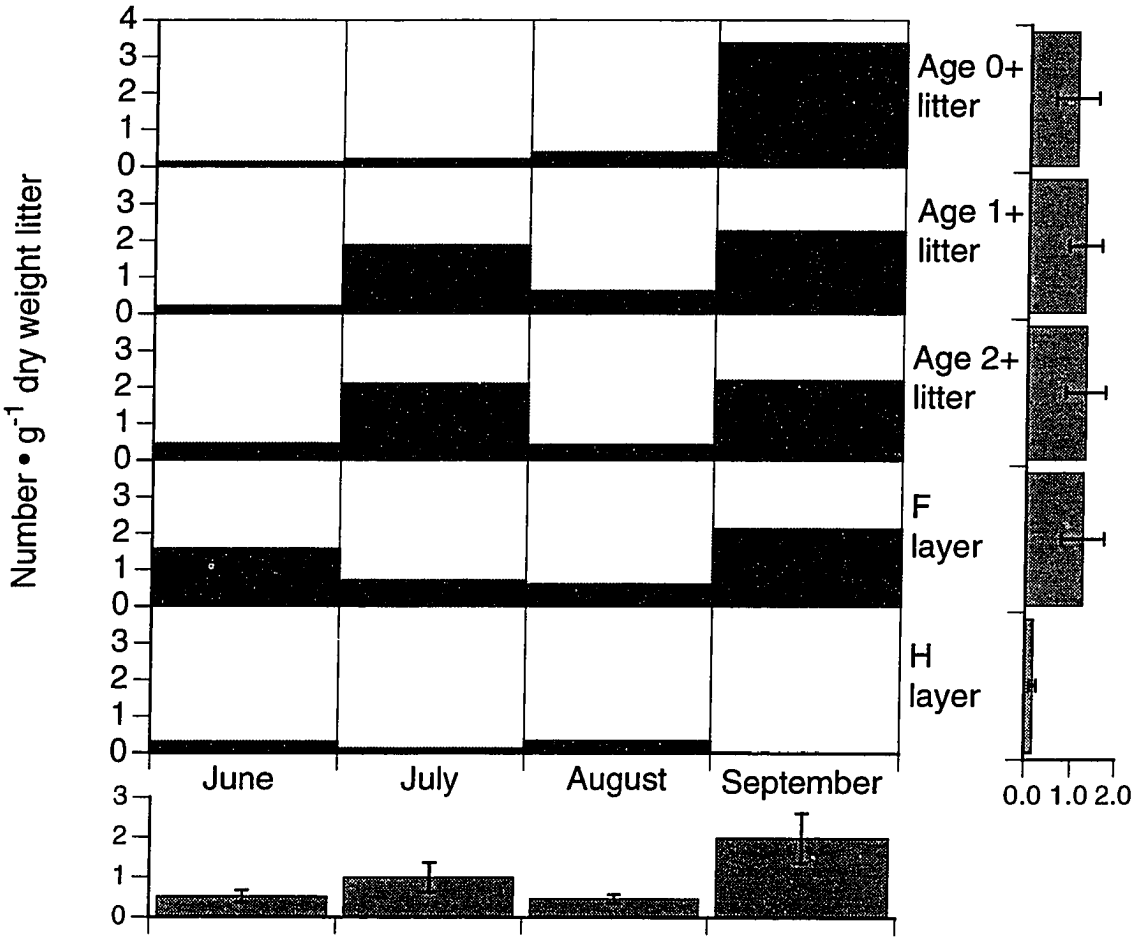

Figure 27. Distribution of *Eremaeus* sp. (Acarina: Oribatida) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

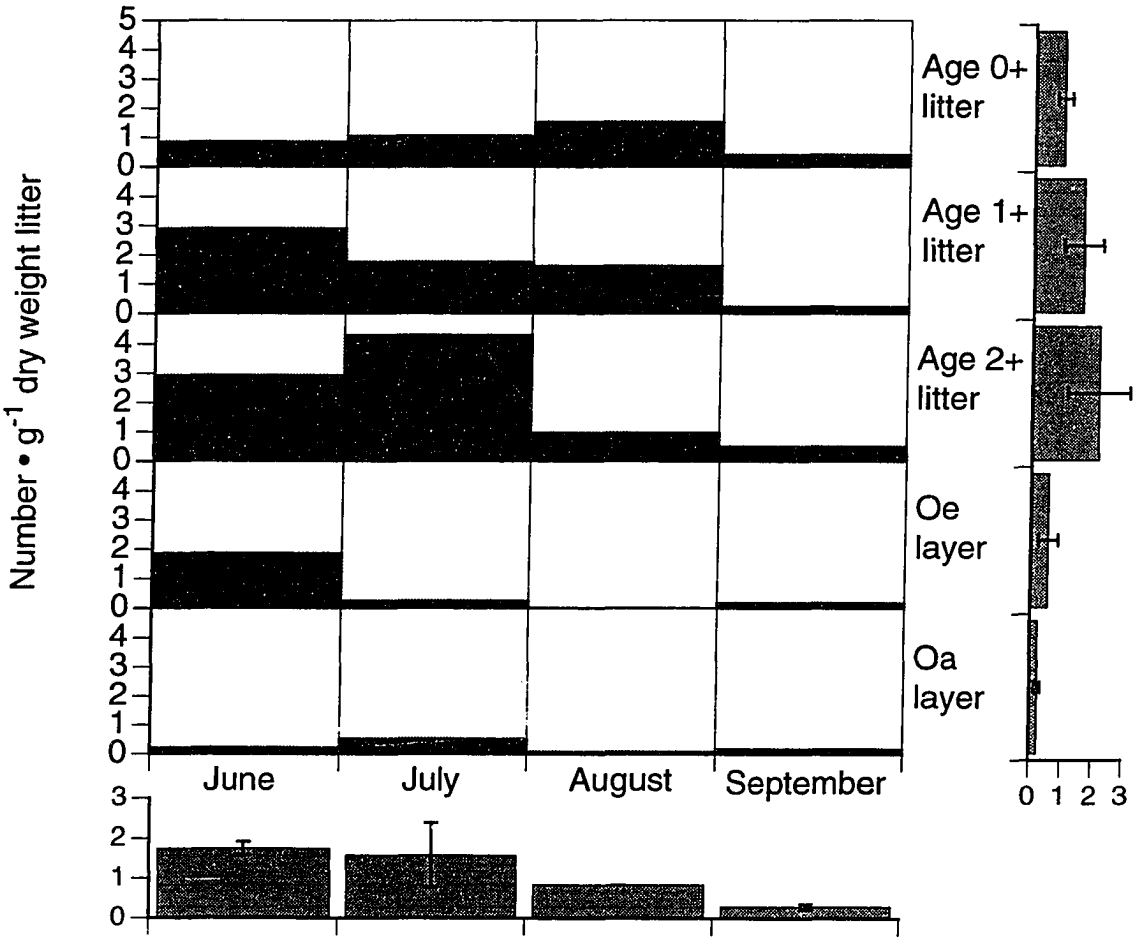

Figure 28. Distribution of *Platynothrus* sp. (Acarina: Oribatida) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

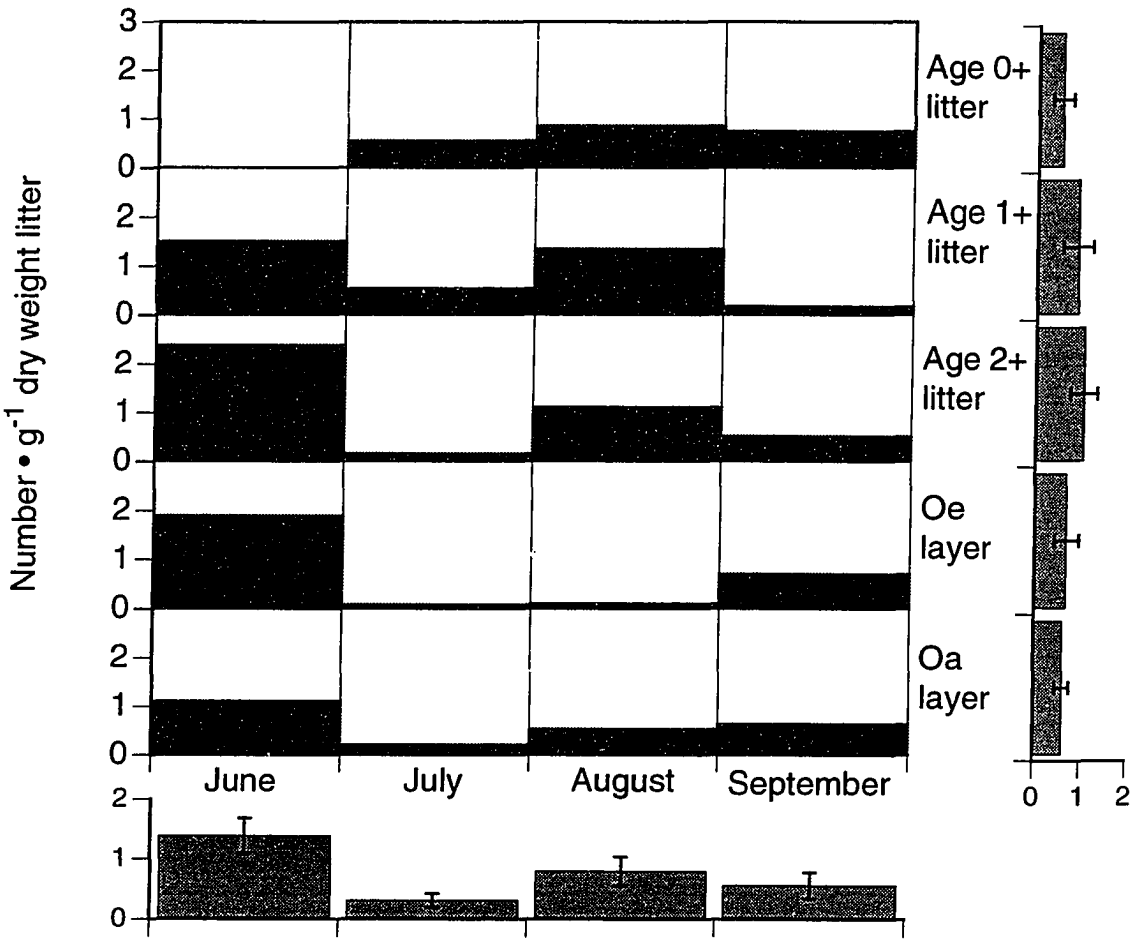

Figure 29. Distribution of *Scheloribates* sp. (Acarina: Oribatida) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

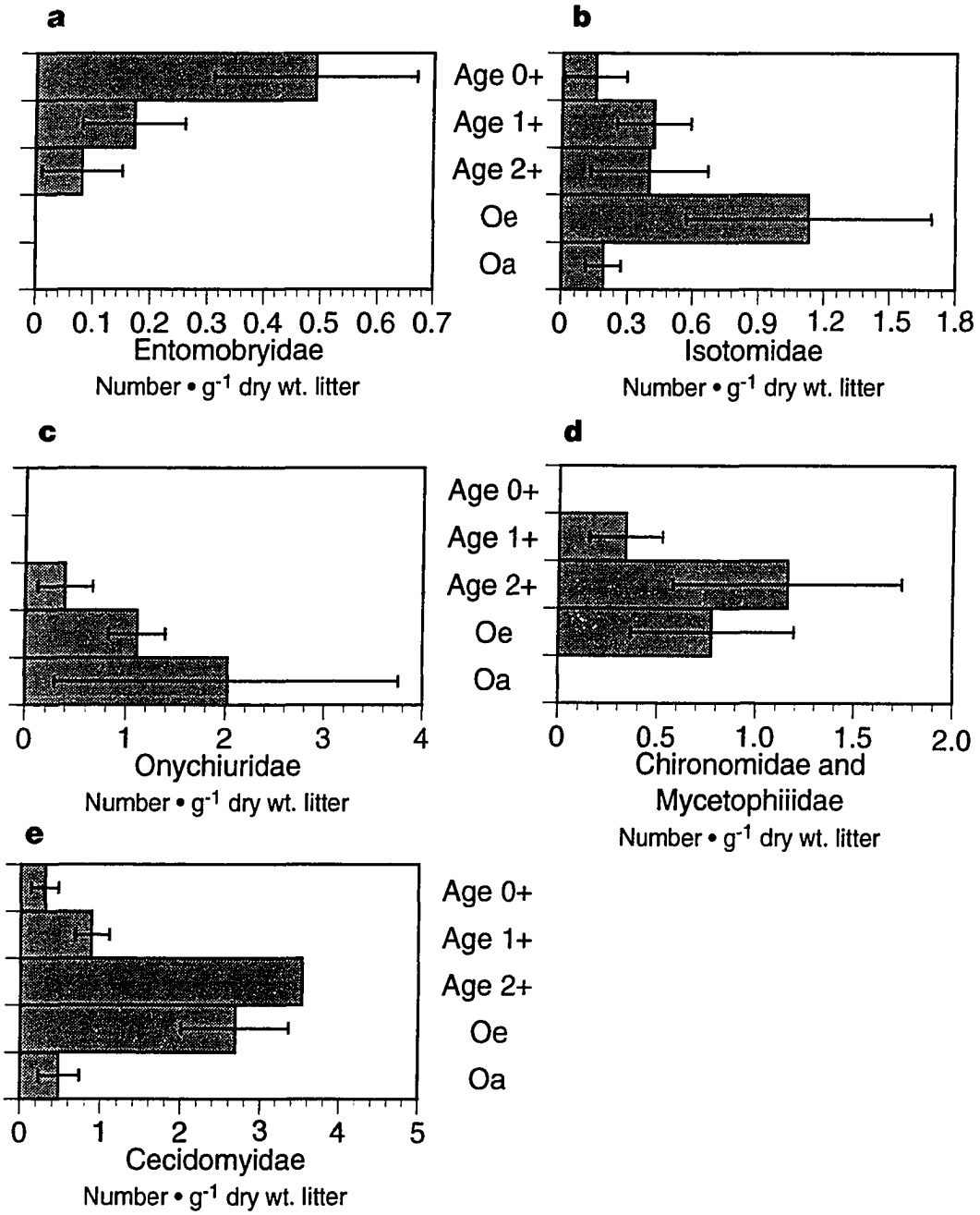

Figure 30. Distribution of Collembola and Diptera larvae in the forest floor strata, September 1992.

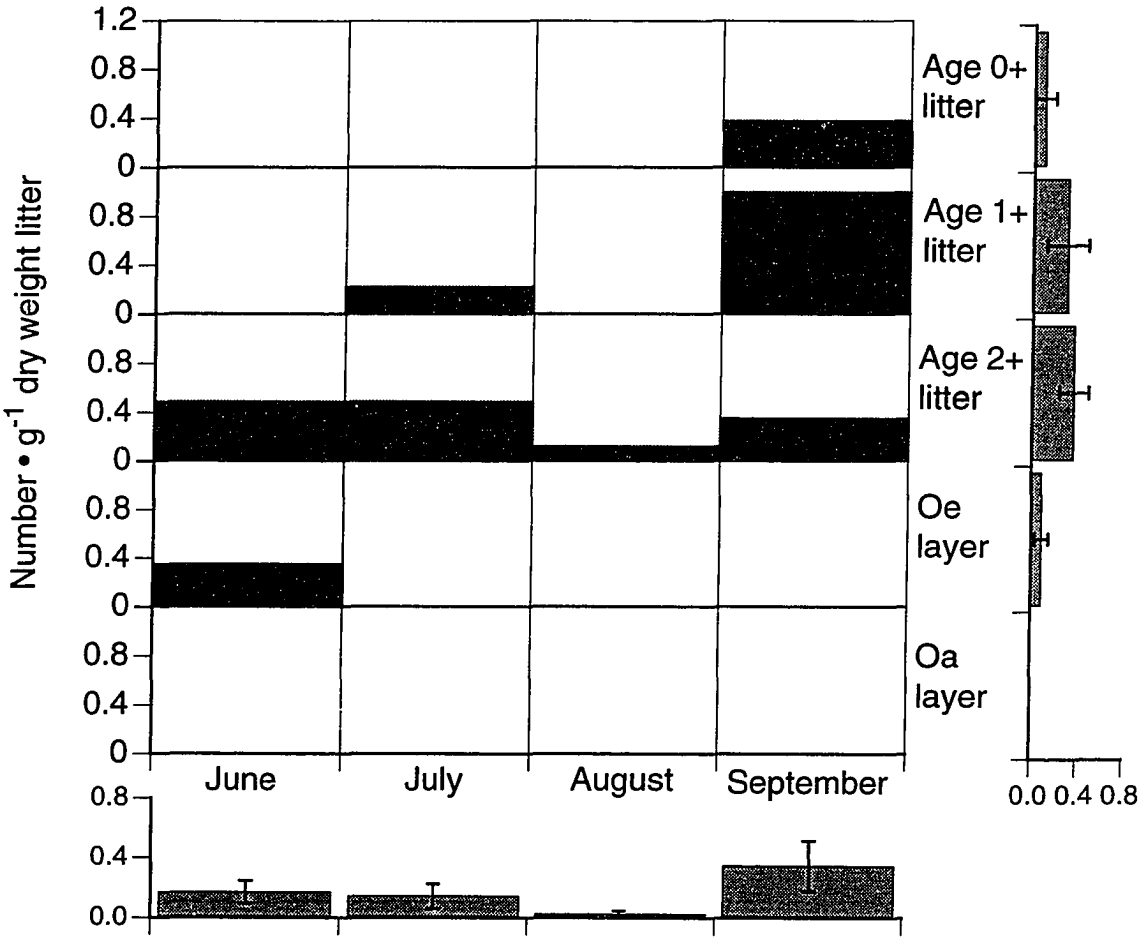

Figure 31. Distribution of Entomobryidae (Collembola) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

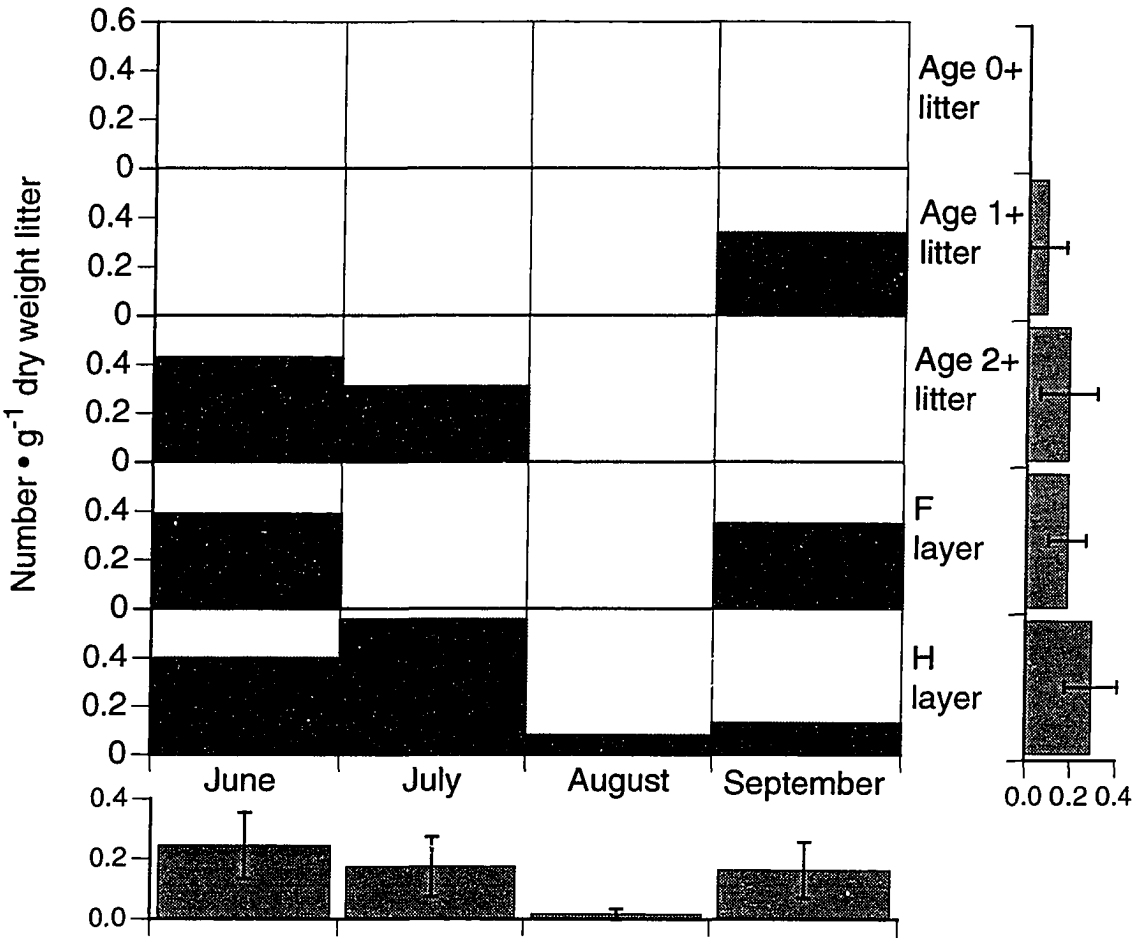

Figure 32. Distribution of Isotomidae (Collembola) in the forest floor strata, 1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

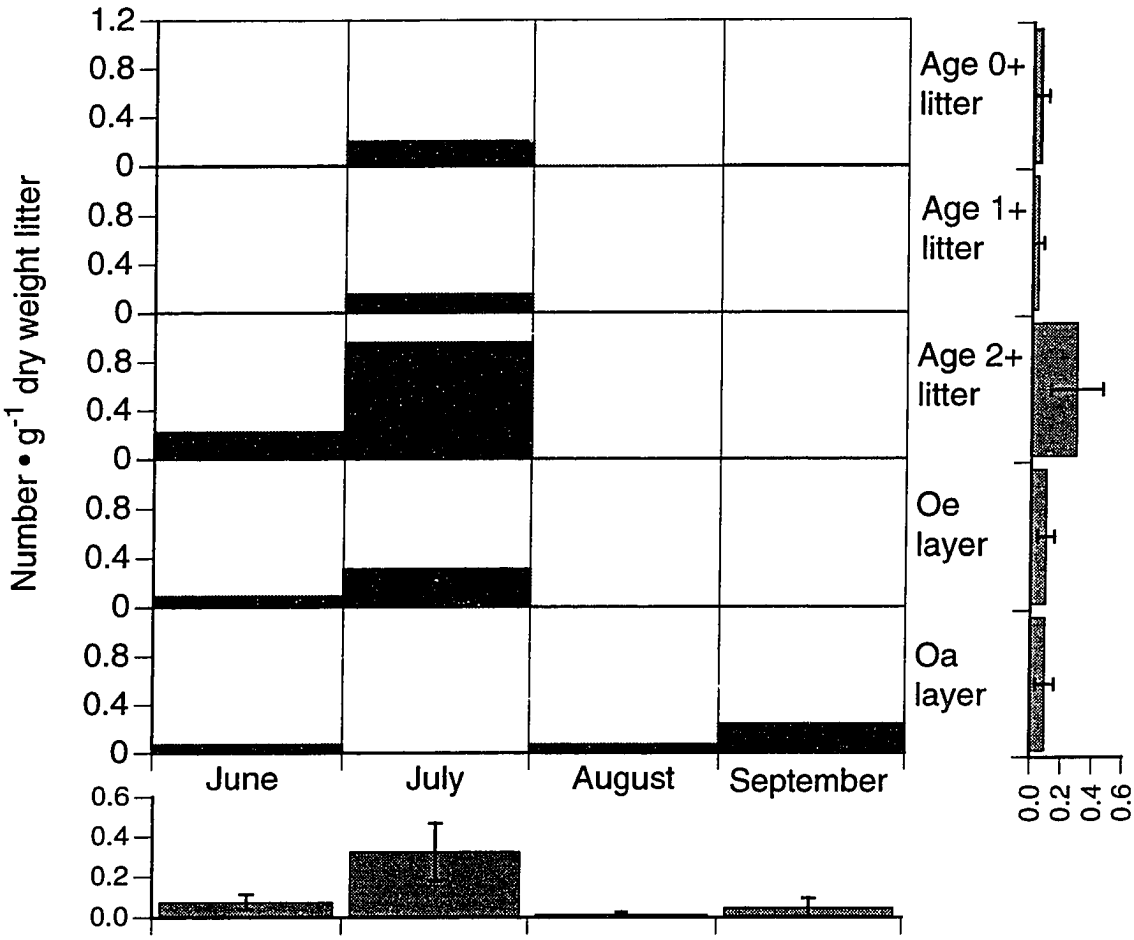

Figure 33. Distribution of Onychiuridae (Collembola) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

Table 4. Composition of dipteran gut contents.

	Leaf Material	Roots	Unidentified
Cecidomyidae	0%	0%	100%
Chironomidae	47	12	42
Mycetophilidae	25	5	70

small numbers and their trophic roles were similar, they were considered together. In September 1992, the litter-eating diptera (Figure 30d) varied with depth ($p = 0.07$). They were most numerous in the age 2+ litter and not present in the top and bottom-most strata. In 1993, litter-eating dipteran larvae (Figure 34) showed no depth or time effect, but they were the most common in the age 2+ litter. Larval Cecidomyidae (Figure 30e) exhibited a significant ($p = 0.01$) depth effect in September 1992. These larvae were most abundant in the age 2+ litter and the Oe layer. In 1993, cecidomyids (Figure 35) varied with depth ($p = 0.05$) and time ($p = 0.01$), with a significant interaction ($p = 0.05$). Cecidomyids were most abundant in the age 2+ litter and the Oe layer, and in July.

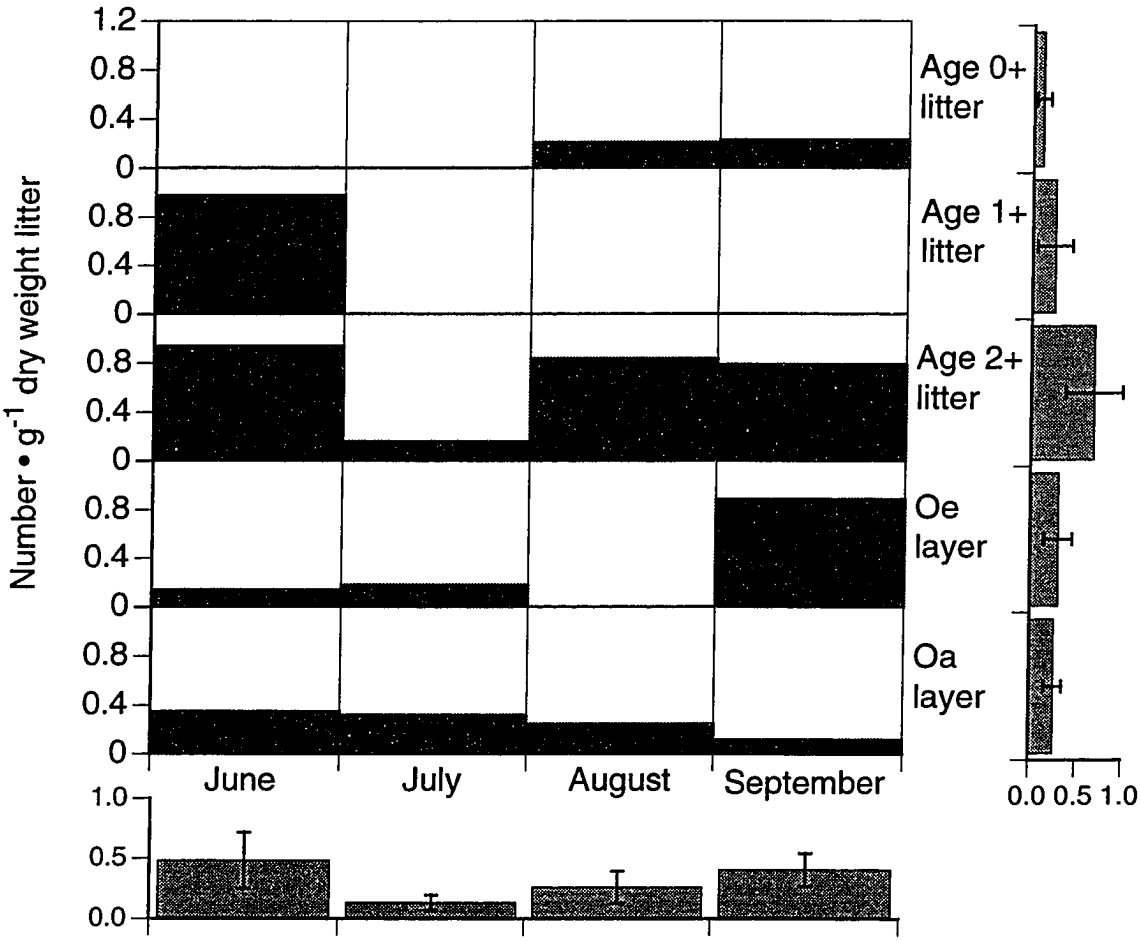

Figure 34. Distribution of Chironomidae and Mycetophilidae (Insecta: Diptera) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

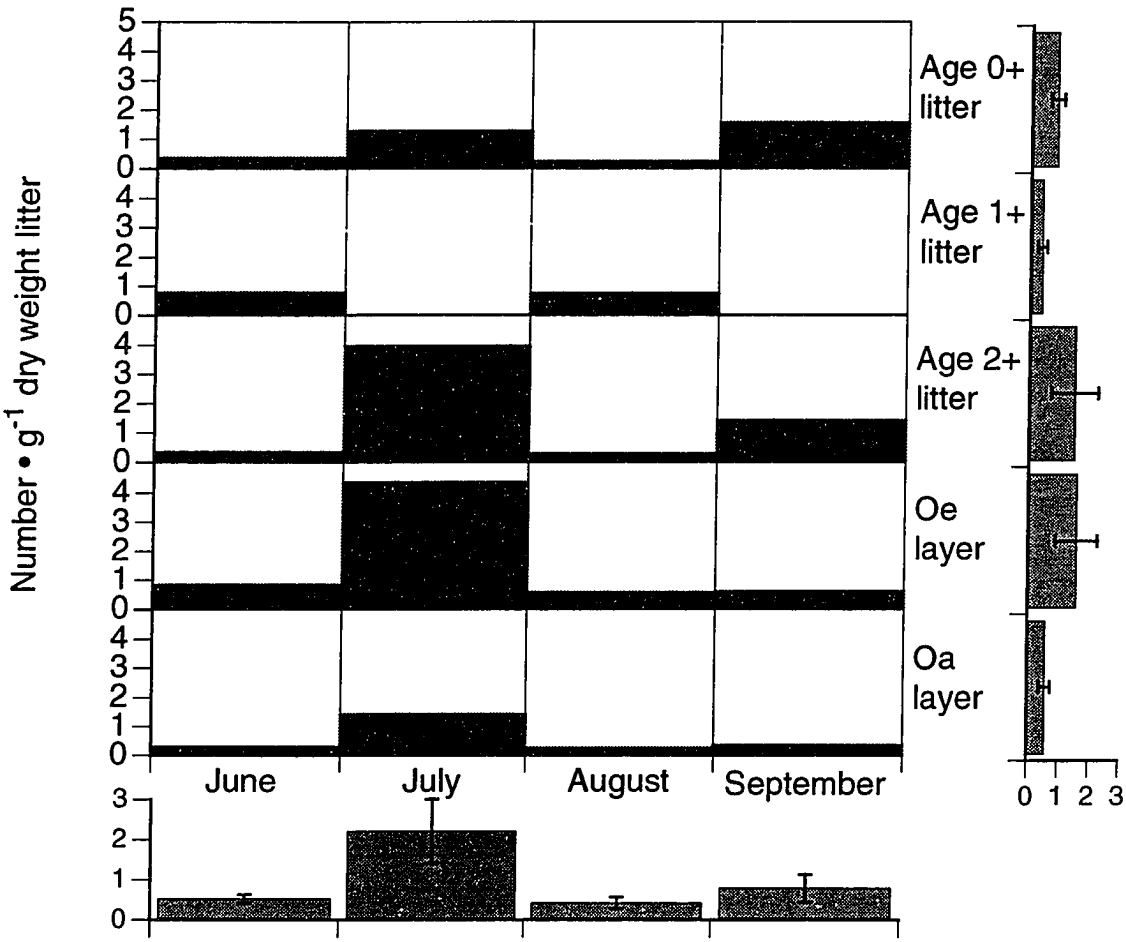

Figure 35. Distribution of Cecidomyidae (Insecta: Diptera) in the forest floor strata,1993. Marginal graphs are cross-time (on the right) and cross-strata (below) arithmetic means with standard error bars. Data shown are based on one sampling date per month.

Discussion

Distributions of soil invertebrate are notoriously patchy in space and time (Petersen and Luxton 1982), likely because of seasonally changing environmental gradients, food resources that are themselves patchily distributed, and faunal life histories. Faunal feeding activities and their role as dispersal agents for microbes (Visser and Parkinson 1975, Newell 1984, Visser et al. 1987) may interact to contribute to the patchy distributions of both microbes and fauna. The fauna distributions are controlled in part by the distribution of the microbes on which they feed. Microbial propagules picked up by feeding fauna are dispersed within the patchy distribution of the fauna.

Three trends in faunal distribution can be discerned from our data: trends in abundance over time, preferences by fauna for certain forest floor strata, and shifts from one forest floor depth to another over time. These trends correspond to the time, depth, and time-depth interactions of our 2-way ANOVAs.

Time effect

Generally, in interior Alaska, May and June are dry, whereas July and August are more rainy. This pattern held in 1993. Typically, microbial biomass—especially fungal biomass—in the taiga forest floor is highly correlated with soil moisture (Moore 1985, Wagener and Schimel, in prep). Several invertebrate groups (stylet-bearing nematodes, tardigrades, and mesostigmatid mites) increased in numbers through summer. Stylet-bearing nematodes and tardigrades, many of which are fungivores (Freckman and Baldwin 1990), are likely responding to increased fungal biomass, whereas mesostigmatid mites (which are predators) may be responding to overall increased numbers of prey (nematodes, rotifers, and tardigrades). Entomobryid collembolans and the oribatid mite *Eremaeus*, both fungivorous (Hågvar and Kjøndal 1981, Valerie Behan-Pelletier, personal communication), also appeared to increase over summer, although the changes

were not statistically significant. Other fungivorous (Walter 1987) taxa—*Platynothrus*, *Scheloribates*, and isotomid collembolans— decreased over summer.

Except for the mites *Platynothrus* and *Scheloribates*, the soil fauna exhibited low numbers in August. The reason for this is not clear. At the same time, high N mineralization potential values were also observed in litter (Wagener and Schimel, in prep.). The peak in N mineralization was likely because of microbial mortality as the litter was rewetting after a dry period. The rapid change in moisture availability which was so stressful to decomposer microbes (Clein and Schimel 1994), may also have reduced faunal populations either directly or indirectly.

Depth effect

The physical, chemical, and biological environment changes with increasing depth in the forest floor (Wagener and Schimel, in prep.). The surface litter (the age 0+ litter) is rich in labile carbon and microbes quickly immobilize any available mineral nitrogen because N limits microbial activity. With increasing depth, the moisture conditions become less variable. The litter has lost more of its labile C and N is less in demand by microbes. In the age 2+ litter, the C:N ratio of the litter reaches a critical point. At this point N is no longer limiting microbial activity and the microbes begin releasing more N than they take up. Plant roots and their associated mycorrhizae begin to appear in response to N availability. Live roots are common through the age 2+ litter and the Oe layer. The Oa layer is composed primarily of root litter and fine particulates eroded from the litter layers and is a poor substrate for microbial activity and biomass. Through most of summer this stratum was the driest litter (Wagener and Schimel, in prep.).

The top stratum is exposed and quite vulnerable to desiccation. The surface litter is the first to dry out, but also the first to rewet after rain. The organisms inhabiting the surface stratum must be able to either survive these varying moisture conditions or avoid them. In general, fauna must survive periodically unfavorable environmental conditions. Most soil arthropods can respond to subtle

differences in microclimate or food availability by moving to a better location (Whitford et al. 1981, Hassall et al. 1986, Moore 1988). In contrast, when environmental conditions are bad, the water-filled pore creatures enter a cryptobiotic state until conditions are again favorable. In cryptobiosis, these organisms can withstand extended periods without moisture and extremes of temperature. In effect, the response of arthropods to poor conditions is to escape in space, whereas the water-filled pore creatures escape in time.

We have observed mycetophilid larvae consuming fresh surface litter in the lab under moist conditions, yet in the field they, as well as most other dipterans, are largely confined to deeper litter strata. Most arthropods have well sclerotized and waxy cuticles and can withstand dry conditions. Larval dipterans, however, are largely unprotected from desiccation and so they—along with enchytraeid worms—are less able to survive in dry surface litter. Because dipteran larvae (Mycetophilidae and Chironomidae) are apparently the only common fauna at our site able to consume litter material, their feeding activities can drastically modify the physical structure of the litter in which they live. Here we see a link between microclimate and litter texture, as moisture limits the distributions of organisms that comminute the litter. The litter therefore remained intact after 2 years in the forest floor indirectly because it was vulnerable to desiccation during this time.

Other taxa demonstrated preferences for particular depths. *Eremaeus* were spread evenly through the top four strata, but rare in the Oa layer. Tardigrade distribution (Figure 23) was centered on the age 1+ litter and uncommon in the Oa layer. The distributions of stylet-bearing and microbivorous-omnivorous nematodes, mesostigmatid mites, *Platynothrus*, and entomobryid collembolans were centered on the age 2+ litter (Figures 28 and 31).

In September 1992, the distribution of collembola was stratified by family. Entomobryidae occurred in the upper strata, Isotomidae in the middle and Onychiuridae in the lower strata (Figure 30*abc*). This arrangement reflects the mor-

phological adaptation of Collembola to soil depth. Entomobryids are pigmented, with prominent eyes, long appendages, and a well-developed furcula. Onychiurids are eyeless, generally unpigmented, with short appendages and a greatly-reduced furcula. Isotomids are intermediate in morphology. In 1993, the differences in distribution were less clear. Entomobryid collembolans (Figure 31) occurred mostly in the top three strata, particularly late in summer. Isotomid collembolans (Figure 32) were present in the four deepest strata, but mostly absent from the age 0+ litter. After reaching a high in abundance in most strata in July, in 1993 onychiurids nearly disappeared in August and September.

Time-depth interaction

Another pattern in distribution, seen in total nematodes, predaceous nematodes, rotifers, and mesostigmatid mites, is a shift from deeper to shallower litter strata over the course of the summer. Whether the "shift" in vertical distribution over time is because of organisms migrating among litter strata or because of different rates of mortality and reproduction among strata is uncertain. Both of these patterns have been noted in soil fauna (reviewed by Luxton 1981). Although mites and large nematodes are mobile enough to move between litter layers, rotifers and small nematodes are quite small, are confined to water-filled pores, and are therefore unlikely to actively migrate. As described previously, this shift in nematodes and mesostigmatids was coupled with an increase in abundance late in summer, possibly in direct or indirect response to a peak in fungal biomass. Tardigrades and entomobryid collembolans appear to follow the same shift in distribution, although the interaction was not statistically significant. Rotifers exhibited the shift in depth distributions without a change in abundance over time. Soil rotifers feed on bacteria and small protozoans in water-filled pores (Wallace and Snell 1991) and are less likely to respond to a big increase in fungal biomass. They may, however, respond to increased litter moisture and the resulting increase in habitat availability.

Soil fauna vary over depth and time because conditions necessary for their survival vary over depth and time. The spatial and temporal distributions of microbial processes and biomass in the litter strata are likely controlled by litter quality, seasonal climate, and the gradient of physical, chemical, and biological conditions with depth in the forest floor (Schimel and Wagener, in prep). The seasonal trends in faunal abundance are not highly correlated with changes in litter quality over time or with decomposition rates (Blair et al. 1990). Because many soil animals can easily move between the litter cohorts, soil fauna populations and their distributions are more closely tied to food (microbes and other fauna) availability and environmental conditions than to the state of the litter.

We have seen that in the birch forest floor of the Alaskan taiga, the distribution of some taxa of soil fauna correlate with depth. In this case the fauna seem constrained mostly by differences in the microclimate of the forest floor strata. Soil fauna may also vary over time in response to differences in the microbial community. Their distributions may exhibit an interaction between depth and time, and they may be responding to a combination of changes in microclimate and changes in food availability. The water-filled pore creatures may also respond to an increase in habitat space as the top-most litter strata become wetter. In the taiga, macroclimate and vertical differences in microclimate exert strong influences on decomposer microbes and are likely also to control (directly and indirectly) the distribution of fauna.

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The effect of leachates from birch litter on microbial processes in the forest floor

Mass loss from decomposing leaf litter is the sum of that because of leaching and microbial and faunal processing. Leaching, in this context, is the abiotic removal of soluble compounds from litter by water. Leaching often begins before the leaves fall from the trees (Van Cleve et al. 1983). After falling to the ground, litter can leach rapidly, depending on precipitation patterns. Deciduous litter can lose up to its 35% of dry mass to leaching (Swift et al. 1979), mostly in the form of cations and simple sugars and proteins. More complex polyphenolic compounds, such as tannin, are also prone to leaching (Irons et al. 1991). Tannin, constructed by the plant largely as a defense against herbivory, inhibits soil microbial activity (Basaraba and Starkey 1966; Baldwin and Schultz 1984; Schimel et al., in review). In contrast, amending soils with sugar or simple phenolics increases microbial activity (Flanagan and Van Cleve 1983;, Sugai and Schimel 1993; Schimel et al., in review). Leachates from deciduous litter might therefore inhibit or stimulate microbial activity in the forest floor, or both.

Because of the absence of macroinvertebrates in birch forests of interior Alaska, litter does not rapidly mix with underlying forest floor material and each birch (*Betula papyrifera*) leaf generally maintains its location relative to surrounding litter for 3 years. Annual cohorts can be distinguished because distinct layers composed of *Equisetum arvense* litter separate the three newest year classes of birch litter in the forest floor. *Equisetum*, because of its texture and the presence of silica in its tissues, leaves a long-lasting residue that provides a sharp visual contrast with birch litter. Below the three clearly defined litter cohorts (strata 1, 2, and 3, collectively referred to as the Oi layer) is the fermentation (Oe) layer (stratum 4), in which the *Equisetum* marker breaks down. Below the Oe layer is the humus

(Oa) layer, consisting primarily of root litter and fine particulates from the Oi and Oe layers.

This clear stratification of litter cohorts in the forest floor provides us the means to study interactions, *via* leachates, between litter at different decompositional stages. During the summer, rain falling to the forest floor wets the top-most (newest) litter and resulting leachates trickle down through litter of increasing age.

Previously (Wagener and Schimel, in prep.), the decomposition of birch litter cohorts has been described as an incremental conveyor, where C is transported vertically—and incrementally—down in the forest floor in the form of plant detritus. N is transported down the profile as organic matter and, at the same time, transported back up to the surface through fungal hyphae. Dissolved and fine particulate C and N can also be lost from each forest floor stratum and be transported down the profile suspended in leachates. This study examines the effect of leachates from new litter on the microbial respiration and C and N dynamics of underlying older litter.

Methods and Material

To examine the effects of leachate flow between litter layers, we conducted an incubation experiment using "cascading" microcosms (Figure 36). The experimental design separated the effects of solutes in the leachates from any effect brought on by water alone. The microcosms, each containing material from one of the five forest floor strata, were vertically arranged and plumbed so that leachates from each stratum directly watered the stratum below it. Thus, a series of five microcosms formed a "cascade" in which leachates flowed from forest floor stratum to stratum as they do in the field.

The microcosms were constructed from ABS plastic pipe and attachment fittings. The body of each chamber consisted of a 170-mm length of 115-mm diameter (101 mm inner diameter) pipe (Figure 36). One end of the body pipe was inserted in a coupler fitting, which served as a base for the microcosm. The other end of the body was inserted in a screw-cap terminator, which served as a closable lid. The threads of the screw-cap were sealed with Teflon® tape. The fittings were sealed with aquarium-grade silicone rubber cement. A plastic funnel—fitting snugly and sealed against the inside wall—was placed inside the chamber. Flexible plastic hose connected the bottom of the funnel to the outside of the microcosm, where the hose was closed by a spring clamp. The volume of the sealed microcosms averaged 916 ml. A sample cup—constructed of a 101-mm diameter ABS coupler with 1-mm nylon mesh sealed to the bottom— rested on the top of the funnel in each microcosm. Sample material was placed on a 1-cm layer of acid-washed silica sand inside the cup. Three holes were drilled in the screw-cap lid: one was covered with a rubber septum, another held a fitting to the hose from the chamber above, and the last was left open for ventilation, except when stoppered during respiration measurements. Water flowing in from above watered the sample material. Excess water then flowed through the acid-washed sand and drained into the funnel, to be carried to the next microcosm chamber.

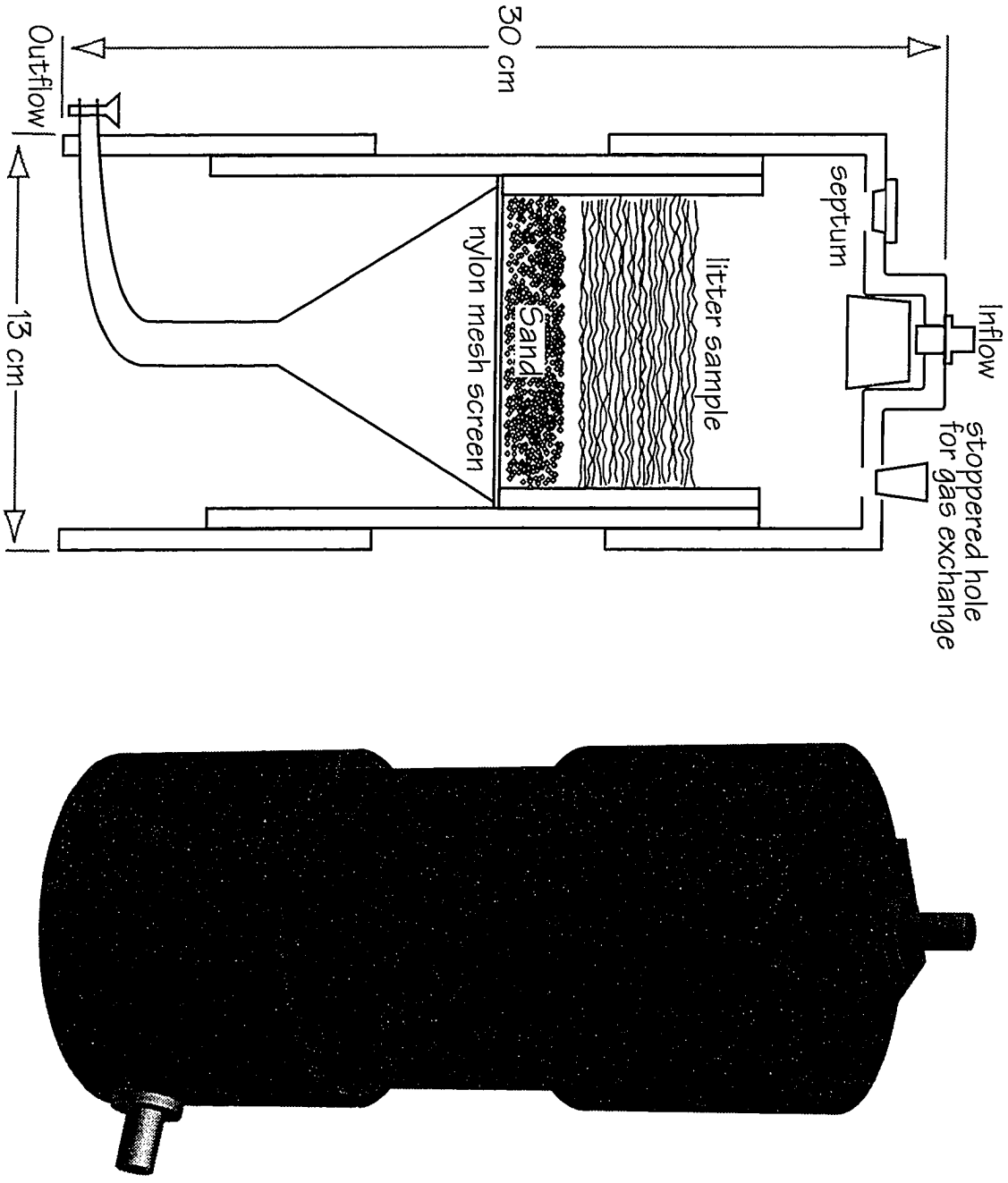

Figure 36. Schematic of microcosm chamber used in cascades.

Ten "microcosm cascades" were constructed, each consisting of five microcosm chambers. In five cascades the chambers were attached in series as described previously, so that water passing through one chamber would flow to the chamber beneath it. In the other five cascade, the chambers were arranged in order of depth, but not connected.

We collected forest floor material from the University of Alaska Arboretum, adjacent to the university campus in Fairbanks, Alaska on 12 September, 1993. The site consists of a near-uniform 100–130-year-old stand of paper birch (*Betula papyrifera*) on the top of a ridge at 144 m elevation. The samples consisted of three separate 0.02 m^2 box cores clustered around each of 3 random points within a 10 meter square grid. We brought the forest floor material into the laboratory and separated it into the five strata (Table 5). *Equisetum* litter served as the marker

Table 5. Year classes (the year the litter fell) of the litter comprising the forest floor strata.

Litter layer	Cohort
Stratum 1 Age 0+ litter	1993
Stratum 2 Age 1+ litter	1992
Stratum 3 Age 2+ litter	1991
Stratum 4 Oe layer	before 1991
Stratum 5 Oa layer	roots and humus

separating the three most recent year-classes of birch litter (the age 0+, 1+, and 2+ litter). Below the age 2+ litter, we defined as stratum 4 the Oe horizon, consisting of the distinct layer of material made up of leaf parts. Below this was a sharp tran-

sition into a zone of fibrous material with few, if any, recognizable leaf parts. The upper 5 cm of this layer was defined as a subsample of the Oa horizon and designated as stratum 5. Material below this was discarded, along with woody debris and course roots from all strata. The entire organic layer is 8 to 10 cm thick. Beneath the organic forest floor is a thick loess layer, which is about 98% inorganic.

The Age 0+ litter consisted of fresh-fallen litter that had been on the ground only a few days. We pooled and thoroughly mixed each material of the same stratum from all nine samples from the box cores. Water content and free-drainage water holding capacity were determined. We placed a weighed (approximately 1 g) subsample of each into a tared aluminum drying pan. Distilled water was added to cover the subsample in the pan and left overnight. The next day the water was thoroughly drained and the pan and subsample reweighed (wet weight). The subsamples were then dried overnight at 40°C in a forced-air drying oven before final weighing (dry weight). From these measurements, we calculated the water content of fresh litter (g H_20 • g dry weight of litter) and percent free drainage water holding capacity (WHC). We placed the following amounts (dry weight equivalent) of forest floor material into the appropriate chambers of the cascades; 3 grams of strata 1, 2, or 3 material; 6 grams of stratum 4; and 9 grams of stratum 5, amounts approximating the relative proportion of material in the forest floor strata.

When watering the connected cascades, we sprinkled 100 ml of distilled water on the litter located in the top microcosm (stratum 1) of each cascade. Water draining from this litter collected in the funnel below and then flowed on to the litter in the microcosm below. Ten ml of the leachates flowing between each microcosms—as well as that flowing from the bottom microcosms—was collected in plastic bottles and stored frozen with the intention of future analysis. In the disconnected (control) cascades, we sprinkled 100 ml of distilled water on the litter located in the top microcosm (stratum 1) of each cascade. Leachates draining from

each microcosm were collected, and an amount of distilled water decreasing by 10 ml with each level of the cascade was sprinkled on the next microcosm. Therefore stratum 1 microcosms received 100 ml of water, stratum 2 received 90 ml, stratum 3 received 80 ml, stratum 4 received 70 ml, and stratum 5 received 60 ml. This decreasing amount of water was intended to parallel the quantity of water— minus the 10 ml samples taken between each pair of microcosms— flowing through the connected cascades. The intent was that the material from connected and disconnected cascades would be exposed to an equal amount of water.

The experiment was conducted in a walk-in constant-temperature chamber in which the temperature fluctuated between 10 and 12°C. The cascades were set up and watered on 1 November, 1993. They were watered again at weekly intervals for the duration of the experiment. At varying intervals through the experiment, gas samples were drawn from the microcosms and analyzed for CO_2 with a Shimadzu GC14A gas chromatograph fitted with a thermal conductivity detector. In preparation for gas sampling, the ventilation holes in the microcosm lids were sealed with rubber stoppers and clamps were closed on the hoses draining each chamber. After 3 hours, a glass syringe with hypodermic needle was used to extract gas through the septa of the microcosm lids. After sampling, the ventilation holes were reopened and the hoses unclamped.

At the end of the experiment on 24 December 1993, the forest floor material was removed from each of the microcosms, dried overnight at 40°, ground, and analyzed using a LECO 2000 carbon and nitrogen analyzer. Analysis consisted of two-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA). Data used in the ANOVAs and ANCOVAs were first rank-transformed (Conover and Iman 1981), to compensate for non-normality. Data were analyzed using Systat software (version 5.2).

Results and Discussion

We intended to analyze samples of the leachates for various dissolved organic compounds, such as tannins, however, it was impractical to analyze such small volumes of dilute leachate. This is related to another difficulty in the experiment. The amount of water flushed through the cascades with each watering far exceed what we would expect after a rain in the field. Because we hoped to analyze leachates, we believed such large watering events necessary in order to obtain sufficient leachates to analyze.

The volume of water used in watering appeared to physically erode the stratum 5 material in the connected cascades. Why this did not occur with the disconnected cascades is unclear. The stratum 5 material is largely root litter and fine particulates filtered down from the leaf litter above: its texture is quite different from that of the leaf litter in the other strata and apparently easier to erode. Perhaps the water flowed with more force in the connected cascades, causing the washing away of the stratum 5 material. The top-most microcosms (containing litter from forest floor stratum 1) of both connected and disconnected cascades were incubated under exactly the same conditions. For these reasons, the analysis of C and N loss from the litter compared only strata 2, 3, and 4.

Comparisons of the litter in microcosm cascades in which the leachates flowed to the underlying forest floor strata (connected) and the litter in cascades where the leachates were replaced with distilled water (disconnected) are referred to as the treatment effect. The depth effect refers to comparisons among litter from the forest floor strata described above and corresponds to the order, from top to bottom, in which the microcosms containing that litter were arranged in the cascades.

These results (Table 6) are similar in pattern to those previously reported from short-term laboratory incubations of these same strata (Wagener and Schimel, in prep.). Microcosm respiration decreased ($p \leq 0.01$) with depth. Respiration rates were relatively constant during the experiment. The connected cascades (except

Table 6. Mean respiration values (μg CO_2-C • g^{-1} dw litter •hr^{-1})of forest floor material in the microcosm chambers and short-term respiration potential values (μg CO_2-C • g^{-1} dw litter •hr^{-1}) of litter strata, September 1993.

Soil Strata	Disconnected Cascades	Connected Cascades	Respiration Potential
Stratum 1	64.65	65.07	102.67
Stratum 2	64.98	53.44	63.54
Stratum 3	31.88	23.90	63.45
Stratum 4	23.98	17.16	22.42
Stratum 5	21.84	21.74	21.40

for stratum 1 and 5) respired less ($p \leq 0.01$) than did the disconnected cascades. The strata-treatment interaction was also significant ($p \leq 0.01$). We see the source of the interaction in the occasional intersection of lines representing the treatments (Figure 37). The differences between treatments did not appear immediately, however. At the beginning of the experiment, respiration rates were similar in connected and disconnected cascades. Only after the third watering on 14 November did the treatments separate. Immediately after the third watering, respiration in strata 2, 3, and 4 in the connected cascades dropped precipitously, a pattern not seen in the disconnected cascades. The extent of the drop decreased with depth. After a few days, differences in respirations had narrowed considerably. After the next watering (21 November), the treatments separated again, but to a lesser degree than before, and only in strata 2 and 3. Again, after a few days the differences again narrowed and stayed relatively constant for the remainder of the experiment. There was no significant difference between treatments in the total loss of litter C or N over the course of the experiment (Figure 38) although a pattern similar to that of the microcosm respiration was seen.

Data from strata 2–4 indicate that leachates from the newer litter suppressed respiration in the litter below. Microbial activity likely played a role in the release

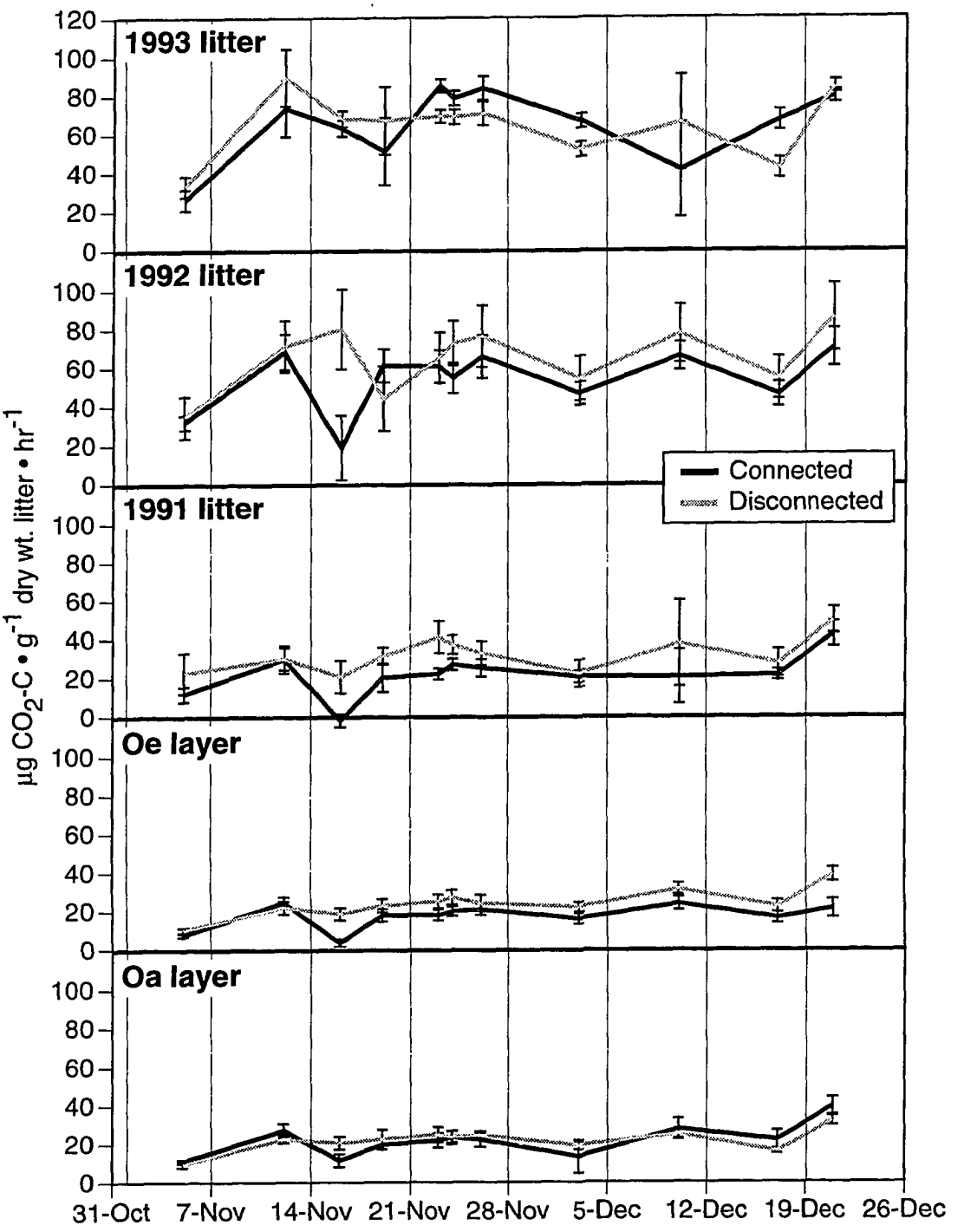

Figure 37. Respiration from microcosms containing litter from birch forest floor strata. Vertical lines indicate watering events. Error bars indicate standard error.

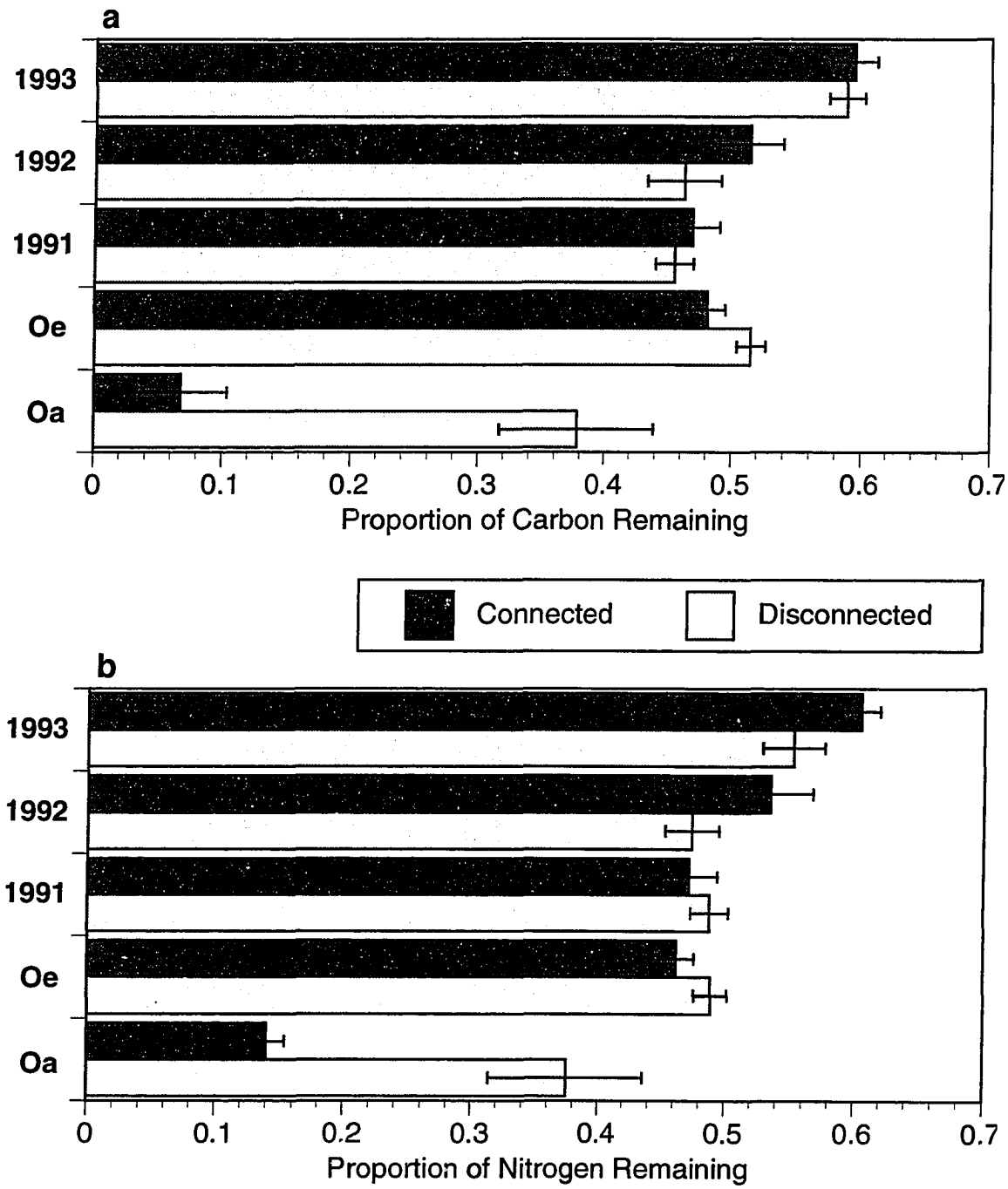

Figure 38. Carbon (a) and nitrogen (b) loss from birch forest floor strata incubated in cascading microcosms. Error bars indicate standard error.

of the suppressing compounds (Stachurski and Zimka 1977), because the effect did not appear immediately. The delay in treatment effect may have been because of initial resistance by the waxy leaf cuticle to both water absorption and leaching (Taylor and Parkinson 1988). Once the cuticle was breached by microbial activity, readily-leachable materials were then exposed to watering. A severe suppression of respiration appeared to be temporary in two respects. After a few days respiration had rebounded and the severity of this "spike" in suppression lessened over time. A lower-level, but statistically significant, suppression of respiration continued through the experiment. Whatever compounds in the leachates caused the lower respiration was likely depleted by subsequent leaching, although chronic effects lingered. Either microbes break down the suppressive compounds or they are absorbed by the organic matter, because the suppression effect decreased with depth and time.

The mechanism by which the leachates may have suppressed respiration is not clear. Sizable concentrations of tannins usually occur in birch litter in interior Alaska (Irons et al. 1988). Tannins inhibit respiration (Schimel et al., in review) and litter decomposition (Basaraba and Starkey 1966). Analysis of subsamples of our litter strata, however, revealed essentially no tannin in the litter material. Whatever the agent, the effect was short lived and had little effect on total litter C and N loss.

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The interactions of substrate quality and winter climate in controlling decomposition of birch litter under Alaskan snow

In interior Alaska, the seasonal and spatial differences in climatic conditions are dramatic. Although summer air temperatures can reach 35°C, winter temperatures can be as low as –60°C, and snow covers the ground for an average of 214 days / year. Overall annual precipitation is low (285 mm in Fairbanks). Within the region, soil microclimate can vary greatly with topography. While a south-facing white spruce forest accumulated 1227 soil degree days (0°C base) during the snow-free months of 1979, a north-facing black spruce stand accumulated just 534 degree days (Slaughter and Viereck 1986). Within the constraints of the cold-dominated environment, substrate quality is an important control on decomposition (Flanagan and Van Cleve 1983).

Winter dominates the phenology of high-latitude ecosystems. Nevertheless, winter soil ecology at high latitudes has received little study and many questions remain. How much litter decomposition occurs during the long winter? How much does litter decomposition vary from year to year? If decomposition does vary, is the variation caused by differences in within-species litter quality from year to year or by annual differences in climate?

Litter decomposition is thought to effectively ceases while the ground is covered with snow. A few studies have examined winter litter decomposition and noted substantial mass loss (Lousier and Parkinson 1976; McBrayer and Cromack 1980; Bleak 1970; Taylor and Jones 1989; Moore 1983) or measurable soil respiration (Coxson and Parkinson 1987; Sommerfield, et al. 1993; Clein and Schimel, in press). Only the last of these studies, however, was conducted in a high-latitude ecosystem and how results of other studies might compare to conditions in the subarctic is unknown.

The quality of litter from the same trees can vary significantly from year to year (Gosz et al. 1972), depending on the age, nutrient status, and stress of the trees that year. Any litter decomposition under the snow occurs in microclimate conditions stressful to the decomposers, because of extremes in temperature and moisture. To what degree yearly variation in winter air temperatures and snow fall might interact with yearly variation in litter quality to control the rate of winter decomposition is uncertain.

In this study we measured soil temperature, snow depth, and C and N fluxes from two yearly cohorts of litter (with different N contents) over three winters (with different patterns in temperature and snow depth) in interior Alaska. The experiment compared different litter cohorts over the same winter and the same litter cohort over different winters to separate quality form climate effects in regulating winter decomposition.

Methods and Materials

This study was conducted at the University of Alaska Arboretum, adjacent to the university campus in Fairbanks, Alaska (64° 51' 36" N, 147° 50' 24" W). The site consists of a near-uniform 100–130-year-old stand of paper birch (*Betula papyrifera*) on the top of a ridge at 144 m elevation. Stands of this age typically have a density of 575 trees · ha^{-1} and basal area of 25 m^2 · ha^{-1}. Tree biomass, annual production, and litterfall average 11156, 470, and 251 g · m^2 respectively (Viereck, et al. 1983).

We raked freshly fallen birch leaves from the ground of the University of Alaska Arboretum soon (for most leaves, one day) after leaf fall in September, 1990. These leaves were dried at 40°C in a forced-air oven, separated from older birch leaves, *Equisetum* litter and other material, and stored dry in cardboard boxes in the lab.

Thirty-five litter bags, approximately 25 cm square, were made from 1 mm mesh polyester netting. Each bag contained ten grams dry weight of birch litter. On 15 October 1990, we randomly placed the bags on a grid (1-m intervals) that covered 100 m^2 of the forest floor. At that time there was approximately 3 cm of snow on the ground and air temperatures were consistently < 0°C. The thin covering of snow was swept from the ground at each spot to allow placement of the bags directly on the forest floor. Five bags were retrieved immediately after placement on the ground, providing samples for determinations of initial values of C and N, minus losses because of handling effects. Ten bags were retrieved on each of three subsequent dates: 1) as soon as the bags were uncovered by melting snow on 6 May 1991; 2) immediately after the first significant snow fall of the next winter, 14 October 1991; and 3) at snow melt, 20 May 1992.

Two additional sets of litterbags, as described previously, were placed on the same grid on 14 October 1991. Seventeen bags contained leaves from the 1990 cohort as noted, and 29 bags contained similarly-collected litter from autumn 1991. Sets of these bags were retrieved: 1) at snow melt, 20 May 1992; immediately

after the first lasting snowfall 14 October 1992; and 3) at snowmelt, 1 May 1993. No bags remained on the ground over all three winters. Upon retrieval, all the litter bags were dried as before, the contents weighed, and set aside for further analysis. The litter samples were ground and analyzed using a LECO 2000 carbon and nitrogen analyzer.

To test the maximum weight loss that could be attributed to leaching, nine 3-g (dry wt.) samples of the 1991 cohort litter were placed in glass dishes and covered with distilled water until the leaves were flexible, the water drained, and the leaves air dried. This process was repeated three times. The litter was then dried for 24 hours at 40°C and weighed.

A data logger (Omnidata) equipped with temperature probes was placed adjacent to the litter bags to record temperatures at 50, 20, 10, and 5 cm beneath the ground's surface and at the its surface. The data logger measured temperatures at all probes at 30-minute intervals and recorded 2-h means during the winters of 1990–91 and 1991–92. Because of the failure of the data logger, soil temperature data from winter of 1992–3 was not available. Four-meter sticks were placed within the litterbag grid as snow gauges. The snow depth was read and recorded approximately weekly during winters 1990–1991 and 1991–92.

Results

Climate

The winter of 1990–91 had the largest snowfall on record in interior Alaska (374.1 cm in Fairbanks, from U.S. National Weather Service data). In early January snow depth at the research site reached 80 cm and remained above this level until mid-April. From late March to early April the snow depth was above the tops of the 1-m gauges. During winter 1991–1992, the snow depth at the site remained below 70 cm. Total snowfall in Fairbanks in 1991–1992 was 249.9 cm. Total snowfall during the winter of 1992–1993 was 353 cm. Snow depth at the site was not measured that winter.

During winter 1990–91, the mean air temperature for Fairbanks during the months of November through March was –18.4°C (from U.S. National Weather Service), eleven days saw air temperatures of ≤ –40°C and 39 days had temperatures < –30° (from site data). The ground's surface, however, cooled below –6° on only one day (Figure 39), and the soil 50 cm beneath the surface did not cool to 0° until 4 February. During winter 1991–92, mean air temperature from November through March was –17.9°C, (from U.S. National Weather Service), but air temperatures (from site data) never cooled to –30°. Despite these warmer air temperatures, the ground's surface fell below –7° on eight dates, and the soil at 50 cm depth reached 0° on 27 November. The mean air temperature for the winter of 1992–1993 was –15.7°

Decomposition

Analysis of variance (with Scheffé pair-wise comparisons) showed that the litter from the 1990 cohort placed on the ground in autumn 1990 lost significant ($p \leq 0.01$) amounts of carbon over both its first and second winter (Figure 40), but the litter from the same cohort (1990) placed on the ground in 1991 lost C ($p \leq 0.01$) during the first winter but not the second. Nitrogen in the 1990 litter placed in 1990 increased significantly ($p = 0.01$) during the first full year; approximately

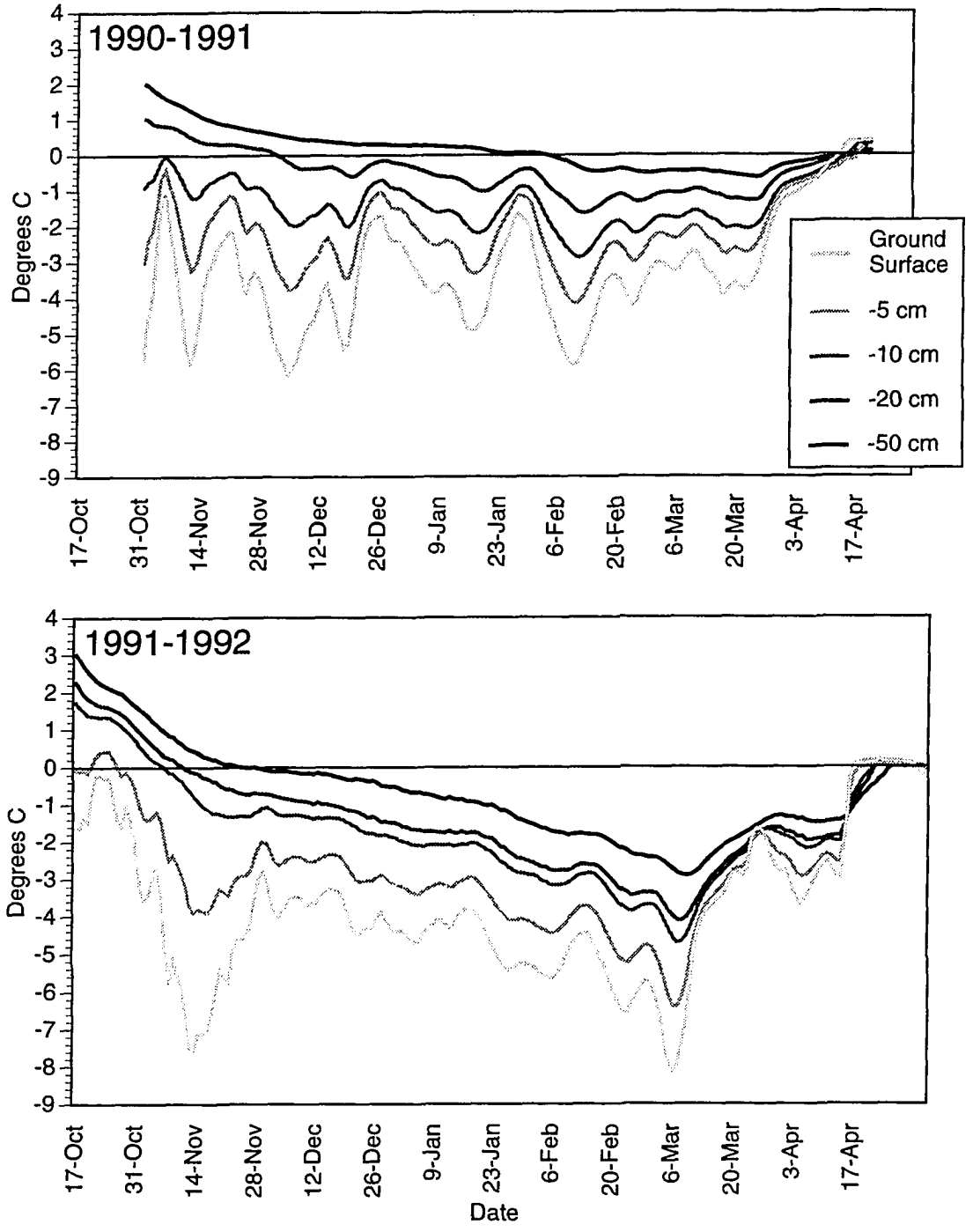

Figure 39. Soil temperatures during the winters of 1990–1991 (a) and 1991–1992 (b).

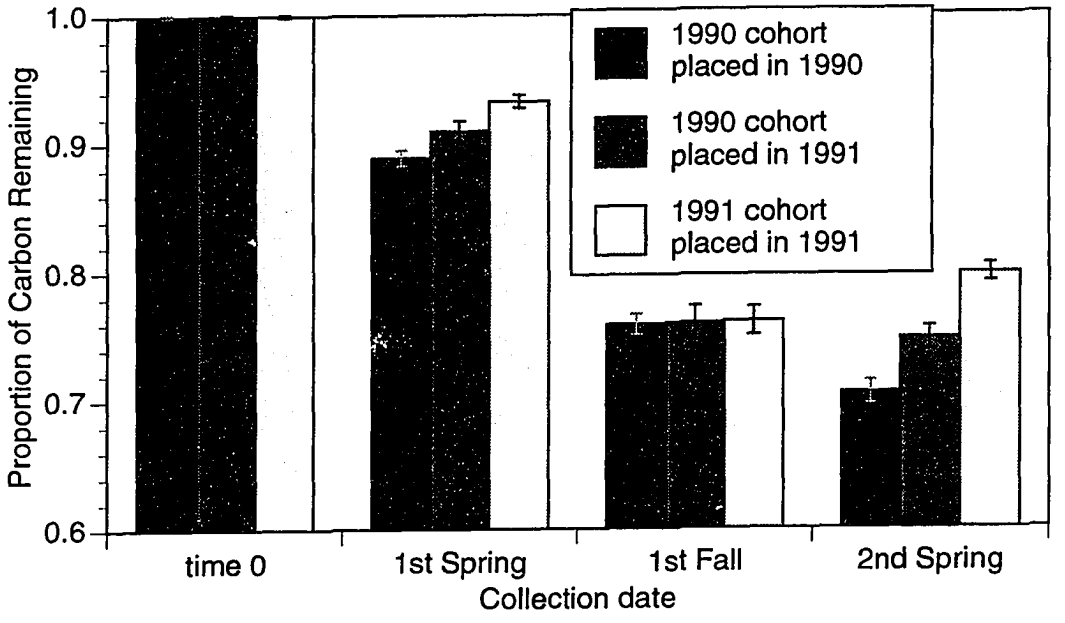

Figure 40. Changes in litter carbon over the winters 1990–1991, 1991–1992, and 1992–1993. Standard error shown as error bars.

one-half of this increase appears to have occurred during winter. Nitrogen in this litter then decreased during the second winter ($p = 0.01$) (Figure 41). There was no difference in N between years of placement. The C:N ratio of the 1990 litter decreased over the first ($p \leq 0.01$), but not the second winter, with no difference between the years of placement (Figure 42). Litter placed in 1991 showed the same basic pattern in N content but with a smaller increase and decrease (Figure 41).

Litter from the 1991 cohort also lost a significant amount of carbon over its first winter ($p \leq 0.01$). There was no difference in C loss during the first winter between the 1991 cohort litter placed on the ground in autumn 1991 and the 1990 litter placed in 1991 (Figure 40). Nitrogen in the 1991 litter increased significantly ($p = 0.03$) during the first winter, but did not change significantly during the second winter (Figure 41). The 1991 cohort litter gained more nitrogen than did the 1990 litter placed on the ground in 1991 during its first ($p \leq 0.01$), but not its second winter. Like nitrogen content, C:N in the 1991 litter decreased over the first ($p \leq 0.01$), but not the second winter. The C:N of the 1991 litter remained consistently higher ($p \leq 0.01$) than the 1990 litter (Figure 42).

All three treatments lost more carbon during their first summer than they had over their first winter. The litter that lost the most carbon over the first winter (the 1990 cohort placed on the ground in autumn 1990) lost the least during summer. Conversely, the litter with the lowest winter carbon loss (the 1991 cohort) had the highest summer loss. Oddly, despite significant differences between treatments (leaf litter cohorts and years) in both winter and summer carbon loss, litter of all treatments had the same amount of remaining carbon over 1 full year of decomposition (Figure 40). None of the treatments gained significant N during the summer (Figure 41). All three treatments showed significant ($p = 0.02$) decreases in C:N over the summer (Figure 42), which was largely because of C loss.

Samples of birch litter from the 1991 cohort leached in the lab lost 7.5% ($\pm$ 0.8) of their mass. There was no significant difference ($p = 0.63$) between mass lost

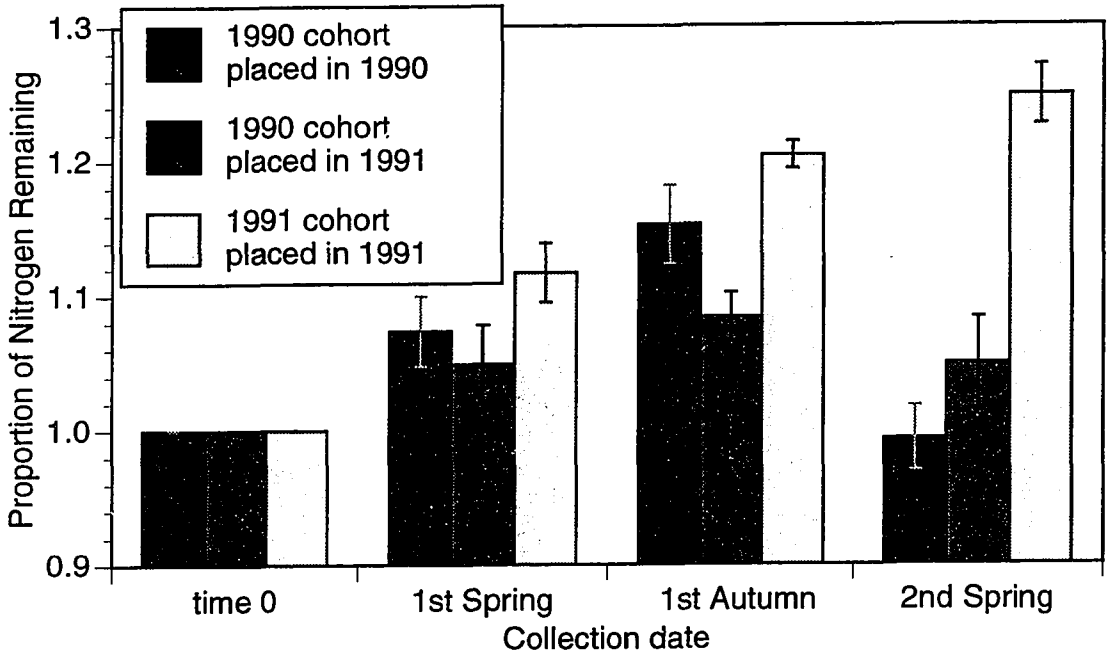

Figure 41. Changes in litter nitrogen over the winters 1990–1991, 1991–1992, and 1992–1993. Standard error shown as error bars.

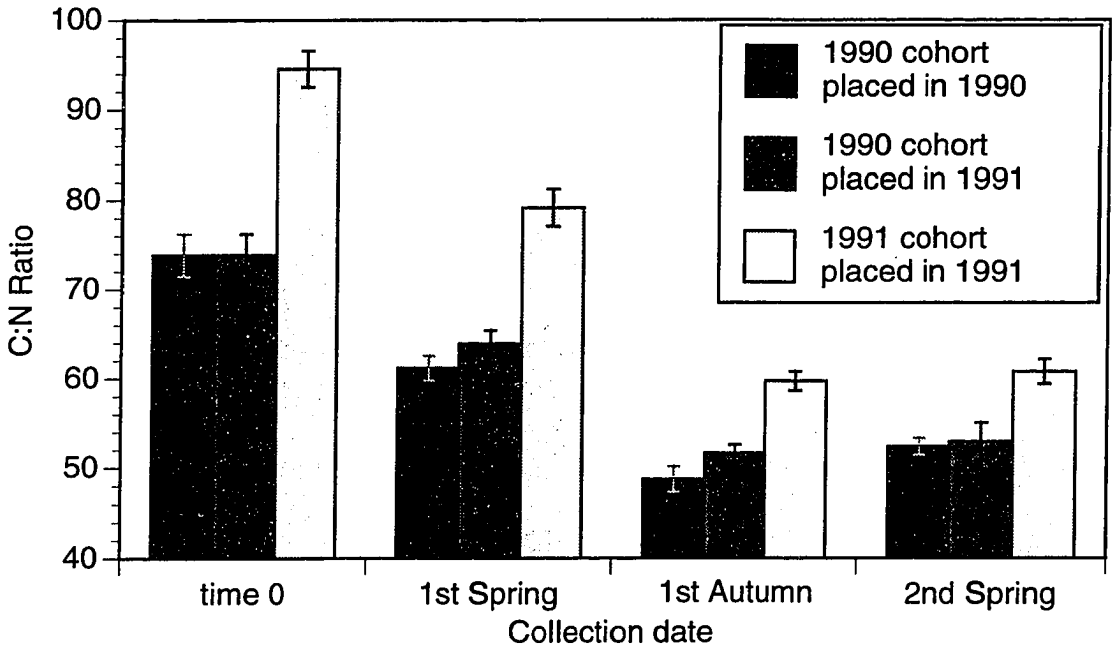

Figure 42. Changes in litter C:N ratio over the winters 1990–1991, 1991–1992, and 1992–1993. Standard error shown as error bars.

from the leaching test of 1991 litter and the mass lost by the 1991 litter during its first winter on the ground.

Discussion

The difference in soil temperatures between the two winters of the study illustrates the effectiveness of snow as insulation. Winter 1990–91 was much colder than winter 1991–92, but snowfall was 50% higher in 1990–91. Despite the colder air temperatures, soil temperatures remained warmer in 1990–91 than in 1991–92 (Figure 39). Winter 1992–93 was warm and snowy, and should have been a favorable winter for decomposition. Throughout both the winters of 1990–91 and 1991–92 there were periodic increases in soil surface temperature, which corresponded to fresh snowfall.That these increases in ground-surface temperature are directly caused by the warmer air temperatures associated with snowfall is unlikely. The insulating ability of snow is at its highest when fresh, and gradually decreases as the snow settles and packs down. The added insulation of fresh snow, blocking heat flow out of the soil, rather than warm air temperature, likely accounts for increased soil temperatures immediately after a snowfall.

The accepted model of litter decomposition in terrestrial ecosystems describes decomposition as being controlled by the interactive effect of environmental conditions and substrate quality on the decomposer biota (Swift, et al. 1979). The experimental design of this study separated year-related climatic influences (combined temperature and moisture regime, as well as duration of snow cover) from cohort-related litter quality influences on decomposition. This design compared the decomposition of birch litter from different cohorts over the same time period with litter from the same cohort decomposing during different periods.

Litter of both cohorts lost carbon during the first winter. Litterbags retrieved in the spring had undergone leaching from snowmelt. Samples of the 1991 litter leached in the laboratory lost similar proportions (approximately 7%) of mass as that observed in the 1991 litterbags in the first winter. N immobilization in the litter indicates that microbial activity, and therefore C mineralization, however, occurred during the first winter. We do not know how the magnitude of the leach-

ing in the field compares with that done in the laboratory, and so can not separate the carbon lost with spring leaching from that because of decomposer activity under the snow.

The heavy snow of 1990–91 led to more meltwater available for leaching in the spring. The 1990 litter lost more carbon over winter 1990–91 than did the 1991 litter over winter 1991–92. The 1990 litter placed in 1991 was not significantly different than either of the other treatments in C loss, but appears to have an intermediate value. The 1991 litter gained N during its first winter. The difference in winter carbon loss between the two years and litters might be because of heavier leaching in spring 1991. Snow can contain N that would be immobilized as it leaches through. This would require microbial activity. The increase in litter nitrogen content results primarily from N translocation from deeper soil (Hart and Firestone 1991). Decomposer microbes must therefore have been active under the snow. Decomposition in the second winter, when leaching should have been complete, also indicates actual microbial activity under the snow.

There was a difference in litter quality between the 1990 and the 1991 cohorts. The beginning C:N of 1990 litter was 73.9 (± 2.1). The C:N of 1991 litter began at 94.5 (± 1.8) and remained consistently higher ($p \leq 0.01$) in all samplings. Although the 1990 litter gained nitrogen through the first year on the ground, it lost a significant amount of nitrogen during the second winter. The 1990 litter placed on the ground in 1991 showed no significant change in N throughout the experiment. In contrast, the 1991 litter appeared to acquire nitrogen throughout the experiment. This points to year-to-year effects of both quality and climate on the N dynamics of winter litter decomposition.

Despite its higher nitrogen content (Table 7), the 1991 litter lost less carbon than did the 1990 litter over the same time period. Litter from the 1990 cohort lost N in its 2nd year of decomposition, whereas 1991 litter continued to immobilize N. This is likely because of the higher C:N ratio of the 1991 litter. The 1990 litter began to lose N when its C:N ratio reached approximately 50, whereas the 1991

Table 7. Initial values of carbon and nitrogen in test litter.

Litter	% C	% N	C:N
1990 litter cohort	47.6	0.6	73.9
1991 litter cohort	47.5	0.5	94.5

litter's C:N ratio never dropped below 60. We therefore predict that this litter would have required another year before it, too, began to lose N.

From this study we concluded the following:

1. There were significant changes in C and N content in birch litter while under the snow. Although leaching during snowmelt could largely explain carbon loss over the first winter, carbon losses in the second winter and the changes in nitrogen content indicate microbial activity during the winter.
2. Both the year-to-year differences in weather and in litter quality played roles in controlling microbial activity.

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Concluding Ruminations

From data presented in this thesis, we may construct a general picture of the dynamics of C and N in the birch forest floor and the forest floor as an environment for decomposition.

C and N Dynamics

An increment of carbon and nitrogen—in the form of leaf litter—enters the decompositional system of the forest floor each autumn. Usually within a few weeks of falling to the ground, leaf litter is covered by snow. Under the snow, the litter is exposed to freezing temperatures and dry conditions. Nevertheless, some microbes are active and the absolute quantity of N in the litter increases (Figure 41). In interior Alaska, snow usually remains on the ground from October to April. Fresh litter is strongly leached by fall rains, ephemeral snows, and spring snowmelt, and may lose 10% of its initial C by the beginning of the snow-free season (Figure 40). Litter on the ground's surface is exposed to extremes of moisture. The normal weather pattern in interior Alaska is to dry in early summer and wet late in summer (Figure 8). Surface litter is the first to dry out, but also the first to wet after rain.

During its first summer on the ground, leaf litter is colonized by microbes, largely fungi seeking labile C. Fresh litter contains C in a variety of forms, some of which—such as carbohydrates and simple phenols—are easily processed by microbes, whereas others—such as lignin and ligno-cellulose—are resistant to microbial activity. Labile C is rapidly respired away from litter by microbes during the snow-free season (Figure 10).

Fresh litter on the forest floor usually has more labile C than can be mineralized with locally available N. Microbial activity is limited by N availability and N therefore is in demand. While N and dissolved organics leached from green

leaves may be available to soil microbes, a larger and more accessible pool of N is available at depth in the forest floor. Fungi attempt to satisfy this N demand in fresh litter by translocating N from sites of net mineralization in the lower strata to sites of immobilization in the upper strata.

The yearly progression of leaf litter cohorts as they move down the forest floor profile may be thought of as a conveyor, or perhaps a "disassembly" line (Figure 43). A cohort of leaves falling to the forest floor remains the top-most layer for 1 year. The decomposition of that cohort occurs under environmental conditions in which the litter can be exposed to extremes of moisture (Figure 8). The next autumn, another cohort falls. The previous top layer is now a step down the profile and its decomposition continues under a different set of conditions, less exposed to climatic extremes. After another year, another cohort falls to the ground. The original cohort is now two steps down the profile and moisture conditions are more stable. By this time, the litter has lost much labile C (Figure 10) and the C:N ratio has narrowed (Figure 9). Microbial activity has slowed and less N needs to be imported for C processing. During this third year of decomposition, N demand decreases to such an extent that N no longer limits microbial activity and microbes begin a net release of N (Figure 11). The timing of N release along the conveyor is largely controlled by the initial N content of the litter (Figures 41 and 42). The remaining C is now more resistant to microbial activity and carbon quality begins to limit microbial activity.

After about 3 years on the forest floor conveyor, the *Equisetum* litter breaks down as a reliable cohort marker, and the litter becomes part of the Oe layer. The approximate mean residence time of material in this layer is two years. During this time, the labile C content of the detritus continues to slowly decrease whereas the N mineralization potential increases.

Fungal hyphae that colonize the top litter strata ride the conveyor over the years as litter passes down the profile. The FDA-active fraction of fungal biomass decreases with depth as it is redeployed to surface litter (Figure 14a). The fungal

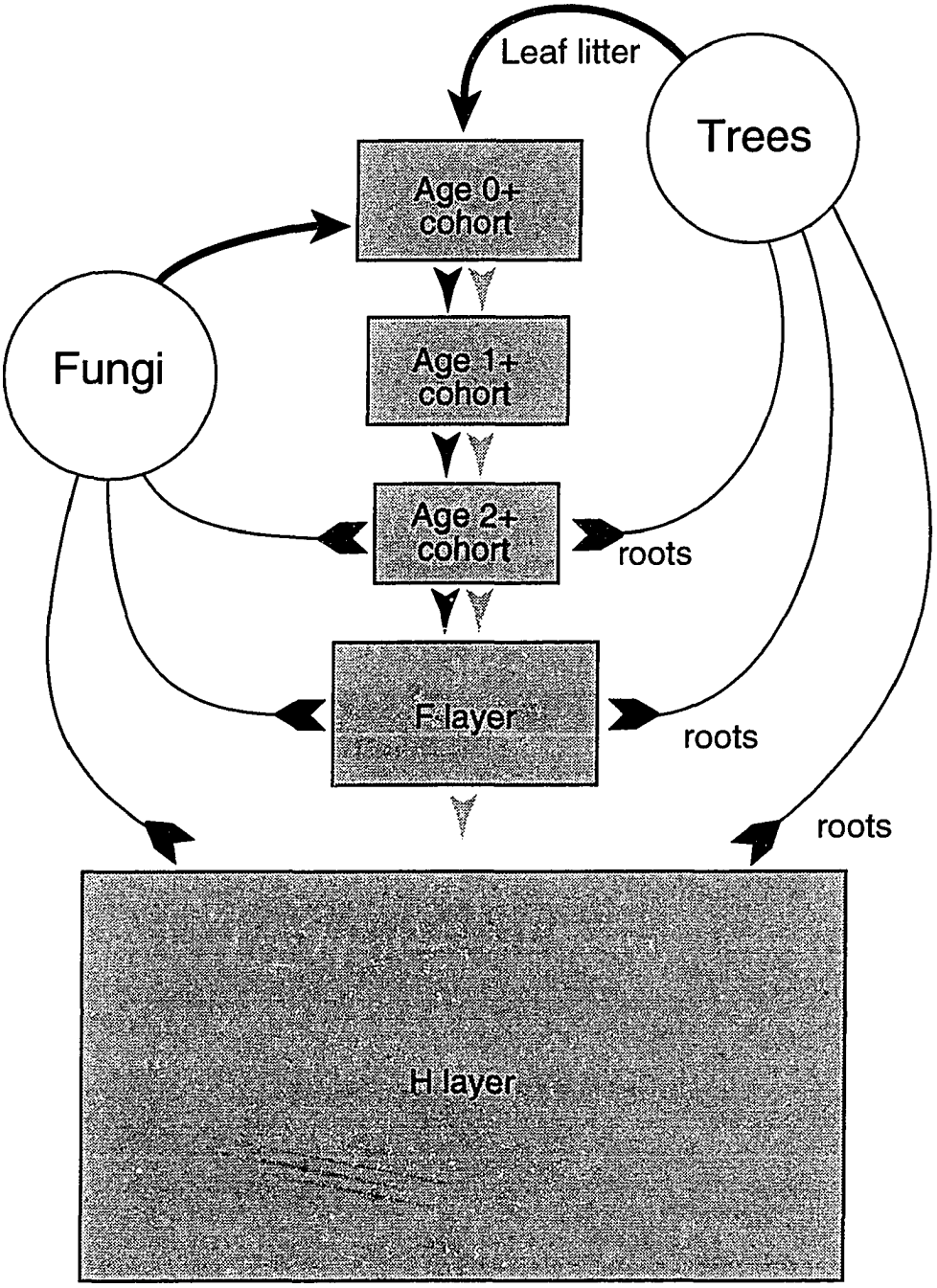

Figure 43. Model of N flows in the forest floor. Boxes representing forest floor strata are proportional to the N pool sizes. Arrows indicate N cycling through biomass. Solid wedges between strata represent yearly incremental movement of N. Gray wedges indicate non-incremental flow of dissolved and fine particulate N to underlying strata.

hyphae are then in place to take up N as it becomes available in the lower strata (Figure 14b). N moves slowly down the profile as detritus, whereas small amounts move quickly up the profile as fungal biomass. Thus we have a set of internal N cycles within the forest floor. The N cycling rate through fungi between the Age 0+ and Age 2+ strata is fairly rapid, perhaps just two years. N from deeper strata is cycled at a slower rate because the turnover of that material is slower.

The litter cohorts are leaky. Dissolved nutrients and organic matter are transported down the profile in leachates. These leachates may affect the microbial activity on underlying detritus (Figure 37). The processing of leaf litter by microbes and the activities of soil fauna increase the surface:volume ratio of the decomposing material and generate fine particles. These fine particles are eroded from all strata and are carried by water down profile or sift down on their own. Material in the Oe stratum has undergone at least three years of physical weathering and fungal processing, both of which can act to break up decomposing litter. This stratum is also the habitat of some of the larger soil invertebrates, enchytraeid worms and larval dipterans, whose movements and feeding activities probably contribute to the rapid detrital fracturing. Erosion is likely the primary mechanism for transport of particulate matter from the Oe to the Oa, which appears to be largely composed of fine particulates trickling down from above and roots both dead and alive.

Also taking up mineralized N in the lower strata are plant roots and their mycorrhizae. Their appearance coincides with the onset of net N mineralization. Much of the N taken up by roots is cycled back to the forest floor as throughfall and leaf litter. The roots themselves, as they senesce and decompose, become sources of mineralizable N for plant uptake and translocation to the surface. Thus, the decomposer organisms always win in the end.

The environment of the forest floor

If we follow the fate of one cohort of decomposing leaves over time, we see that the microbial breakdown of leaf litter is a gradual process. The labile carbon content gradually goes down as the nitrogen content (at least initially) gradually goes up. While the rates of elemental loss may change through the course of decomposition, the flux of C and nutrients to and from a single cohort of litter can be viewed as a continuum. This generally linear change in litter state is the view of decomposition we get from litterbag studies.

During the extraction of nutrition from forest floor material, the biota directly change both its quality as a substrate and its physical characteristics. Microbial processing and animal activity increase the surface area of the decomposing material. A higher surface:volume ratio means more total living space for microorganisms and more diverse microsites for organisms with specific environmental requirements. Therefore, over the first several years of decomposition, the quality of litter as a substrate (for most microorganisms) decreases as its quality as a habitat (for most microorganisms) increases. In the later stages of decomposition, organisms literally eat themselves out of house and home.

Although the changes within a single cohort may be continuous over time, the among-cohort changes in litter quality and microclimate encountered by a soil organism—animal or fungal—as it moves between litter cohorts in the forest floor are incremental (Figure 15). A litter cohort is exposed at the surface for an entire year, then covered by another cohort for another year, and so on, so that the cohort's environment, its climatic buffering and exposure to litter-comminuting invertebrates, also changes incrementally. Since each cohort in the forest floor is a year less decomposed than the litter directly below it, N availability also increases incrementally with depth.

The distributions of many organisms are constrained by the vertical stratification of the birch forest floor environment. The ratio of fungi to bacteria narrows with increasing depth (Figure 14). Bacteria are limited by the C and nutrients

available at their microsites. They live in water-filled pores and must enter a resting state when conditions are unfavorable. The deeper strata, with a less variable microclimate and more available N, therefore provide a favorable habitat for decomposer bacteria. The fungi, however, are larger and much more tolerant of dry conditions. At any given time much of the total fungal biomass is inactive and fungi can allocate metabolically active protoplasm to hyphae near good resources and favorable conditions. Fungi can also be in many places at once and can transport a resource, such as nitrogen, from where it is available to where it is needed. The fungi are thus able to exploit the upper strata, where climate is variable and N is in demand.

While many soil fauna (most of the arthropods) are able to move to a new and better location when conditions are poor and resources depleted, others (organisms that live in water-filled pores) are quite small and are limited to sites circumscribed by substrate and the water surface tension. Like bacteria, when their environment changes for the worse, these organisms must enter an inactive, resistant state until conditions are again favorable. Some of the semi-aquatic organisms (enchytraeid worms, dipteran larvae, and the largest nematodes) are large enough to break the constraints of surface tension and move about freely in the forest floor. They are not, however, free of water because they take their own water films with them and must stay in the moister litter layers. The enchytraeids (Figure 24) and most larval dipterans (Figures 34 and 35) are generally constrained to the Age 2+ and Oe layers, where their movements and feeding activities may contribute to the breakup of litter fragments. The distribution of each group of organisms would then be determined by the intersection of the regions where then can find food, and where they can find habitat.

While within-cohort continuous and among-cohort incremental changes are both unidirectional, weather patterns (Figure 8) and the response of the decomposer microbes are cyclical. The biomass and activity of fungi increases with increased soil moisture in the fall (Figure 12). Fungivorous animals (Figures 19,

28, and 29) may also respond to the cyclical changes in soil climate and microbial biomass.

These three sorts of environmental gradients—continuous, incremental, and cyclical—are interrelated. Each temporal cycle corresponds to an spatial increment of environmental change. The amplitudes of the cyclical changes in moisture and microbial biomass are modified by depth as the litter is less vulnerable to drying and as labile C disappears. The incremental contrasts we perceive between litter cohorts are an orthogonal slice from a stack of continua. Any factor, such as initial litter quality, affecting the exact location of the cohort along the continua of state or process will also affect the degree of contrast between adjacent cohorts.

It is reasonable to ask how well this model would apply to other birch soils in the taiga. While the use of this specific experimental approach would depend on the presence of a reliable natural marker (*Equisetum* or other suitable litter) and the absence of soil macrofauna, the controls over C and N dynamics and organism populations described here likely apply broadly. In taiga ecosystems, climatic variables are both the overriding control over processes and themselves quite variable across the landscape. Climate surely drives differences in soil processes among similar taiga forest stands. Differences in moisture regime should influence patterns of microbial biomass and processes, which would then control the distributions of fauna.

Clearly, the forest floor is a fascinating system for ecological study. To see a full measure of its complexity and inner workings requires a view of fine resolution into the spatial and temporal scales of its processes. Our method of examining the forest floor material as individual cohorts of litter is a step toward understanding decomposition and nutrient cycling.